LIFE HISTORY OF THE GIZZARD SHAD, *DOROSOMA CEPEDIANUM* (LE SUEUR), IN WESTERN LAKE ERIE

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ABSTRACT

The rapid increase in the stocks of gizzard shad in Lake Erie since 1950 unquestionably had an important effect on the ecology of the lake. The present study, based on almost 24,000 fish collected by various means in 1952–55 in or near the island area of western Lake Erie was undertaken to provide information on the role of shad in the bionomics of the region.

The annulus of the gizzard shad scale is a valid year-mark. It is laid down in May–July, a little later in the older than in the younger fish. The body-scale relation is linear with an intercept of 22.1 mm. on the axis of standard length. Age-groups 0, I, and II were abundantly represented in the samples. Age-group III was much less well represented, and older fish were extremely scarce. The oldest shad seen belonged to the VI-group.

The seasonal growth was most rapid in July–August and growth was much reduced or nil in January–April. Males attained the following average standard lengths (in millimeters) at the end of the indicated years of life: 1–141; 2–273; 3–313; 4–343; 5–349. For females these values were 1–140; 2–285; 3–335; 4–364; 5–386.

The weight of the gizzard shad increased as the 3.07053 power of the length. The length-weight relation varied seasonally, annually, and, near the spawning season, according to sex and state of gonads.

Only a few precocious male and female gizzard shad attain sexual maturity as age-group I. Almost all males and a good percentage of females mature at age II and only rarely are III-group shad immature. Development of the egg and seasonal changes of the ovary are described. Egg production is highest in the II group—average of 378,990 per individual and 689 per gram of body weight. Spawning takes place from early June into July and is most intensive near mid-June. Heaviest spawning is at water temperatures of 67° F. or more. Early development to the attainment of the adult shape is described; particular attention is given to the development of the alimentary tract.

The anatomy of the digestive tract in the adult is described, and comments are offered on the function of such organs as the pharyngeal pouches and the caeca. Tests were made for digestive enzymes in different parts of the tract. The gizzard shad is a filter feeder. Food varies widely with season and locality but consists mostly of phytoplankton and zooplankton.

The role of the gizzard shad in the ecology of fish populations is difficult to assess. Its value as a link in the food chain is not to be questioned. On the other hand, no use for shad other than as forage fish has been developed and their rapid growth soon makes them too large for most predatory fish. Shad tend to overpopulate many waters to a degree that seems to be detrimental to other species. In some southern states reduction of numbers of shad is part of the fish-management program for certain waters.

In the past years, the numbers of gizzard shad in Lake Erie were too few for the species to create any important problems, indeed, to have any real significance in the bionomics of the lake, but recently their abundance has increased enormously. Mass mortalities have created esthetic and public-health problems, water intakes have been plugged, and commercial fishermen have wasted hours sorting and discarding the worthless shad from their catches. From the fish-management standpoint, the question arises whether the value of shad as forage may not now be outweighed by their diversion of the productive capacity of the lake into commercially valueless fish. An inquiry into the natural history of the gizzard shad in Lake Erie, accordingly, has been much needed.

Although the gizzard shad is distributed widely throughout the Mississippi Valley and

NOTE.—Approved for publication August 13, 1964.

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in stream systems tributary to the Gulf of Mexico and the Atlantic Coast north to about lat. 40° N., some question exists as to whether it is native to the Great Lakes-St. Lawrence basin or has penetrated in this region in historic times. Gerking (1945) was of the opinion that this fish migrated from the Mississippi drainage into the glacial Great Lakes during the Lake Maumee outlet stage. Kirtland (1850) believed that it gained access to Lake Erie from the Mississippi drainage recently by way of various Ohio canal connections. Trautman (1957), on the other hand, thinks that the gizzard shad was present in Lake Erie waters before the advent of the canals. Miller (1957) believed the question of whether the shad is native to Lake Erie cannot be solved conclusively.

The establishment of gizzard shad in Lake Erie in large numbers appears to have taken place fairly recently, however, and their presence in Lakes Huron, Michigan, and Ontario became known subsequent to collections of the species along the south shore of Lake Erie. The report of gizzard shad in the St. Lawrence River at Quebec is of recent date. Freshwater fishery investigations—especially of rough fish—were so meager prior to 1850 that shad could easily have been overlooked.

In the Great Lakes-St. Lawrence drainage the gizzard shad has been reported from Lake Michigan in the west to Quebec in the east, but it has become best established along the western and southern shores of Lake Erie and in streams tributary to these shores.

The gizzard shad population has been increasing in Lake Erie. Commercial fishermen told me that 3 decades ago the "sawbelly" was something of a rarity—only an occasional one was caught. They have attained greatest abundance, according to these fishermen, since about 1950. Whether this increase results from adaptations to the Lake Erie environment, to changes in the character of the lake, or merely to increasing surpluses of shad beyond environmental and predatory inroads has not been determined.

Gizzard shad seem to be most plentiful in the shallow waters around the periphery of western Lake Erie, in the Bass Islands area, and especially in protected bays and mouths of tributaries. The numbers present here vary from season to season. They are most numerous in late summer and early fall when their abundance is increased by the recruitment of the young of the year. They are next most plentiful just prior to and during their spawning season in late spring when the mature shad congregate in the shallow waters. Then, too, in winter they concentrate in places into which warm streams flow. At other times they are rarely seen in numbers—frequently days go by without any captures of shad by the commercial fishermen of South Bass Island.

The tendency of shad to inhabit shallow water, their attraction in massive numbers to the warmer water of outlets from industrial plants and of inflowing streams, and the frequent mass mortalities doubtless have given rise to an exaggerated idea of their abundance. Nevertheless, they are plentiful and their numbers are growing. The shad problem is real in both a practical and a purely scientific sense.

MATERIALS AND METHODS

The investigation of the life history of the gizzard shad was based on almost 24,000 fish (about two-thirds of which were young of the year) captured in western Lake Erie and in streams tributary to the southwestern shore of this lake in 1952–55. Studies of age, length, weight, growth, reproduction, and fecundity were made for shad captured in the lake. Fish caught in Sandusky Bay and in the tributary streams were omitted from those phases of the study because of differences in growth and other aspects of their life history.

The Sandusky Bay specimens were decidedly smaller than lake fish of the same age and appeared to have formed their annuli earlier in the year. Also, they probably spawned earlier than the lake-dwelling gizzard shad. The water in Sandusky Bay was frequently turbid — the shallow water is readily turned over by winds. Phytoplankton, though reduced by this turbidity, is not lacking, for much is washed into the bay from the marshes by the tributary streams. Stomach contents of fish caught in Sandusky Bay were largely muddy. The slower growth of the fish here probably

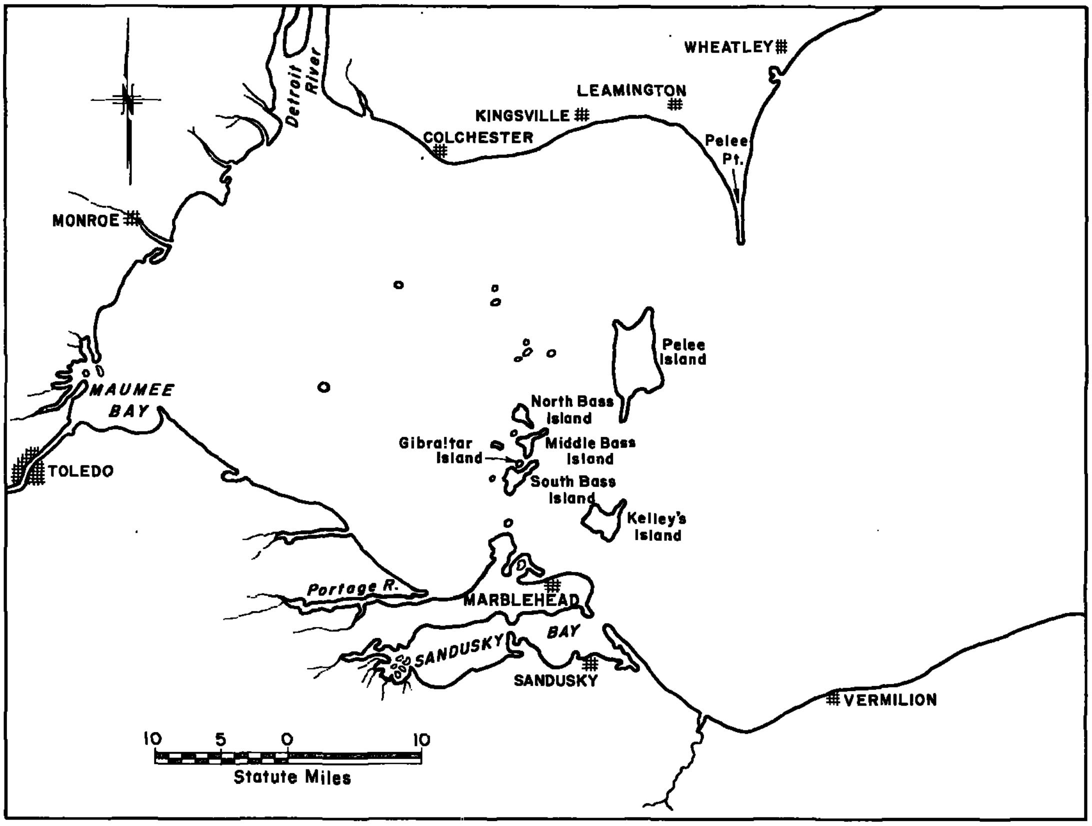

FIGURE 1.—Western Lake Erie where gizzard shad were collected in 1952–55.

resulted from the reduced nutriment. The earlier annulus formation and spawning are undoubtedly related to the earlier warming of the shallow waters in the bay.

The gizzard shad caught in the streams were not as deep-bodied as either the lake or the Sandusky Bay fish; and they were smaller, age for age, than those captured in Sandusky Bay. They were thinner, more gracefully shaped individuals, seemingly better adapted for swimming in streams. Probably the colder water and the poorer food supply were responsible for their slower growth.

Methods, Dates, and Sites of Collection

With the exception of gizzard shad from Sandusky Bay or tributary streams and a few otter trawl collections in the open lake, all samples were captured in western Lake Erie within one-half of a mile of island or mainland shores (fig. 1).

Gizzard shad were captured in the deeper water by 5-inch mesh (stretched measure) gill nets and standard commercial trap nets. Closer to shore, in 4 to 10 feet of water, I collected them by means of 4-inch mesh gill nets, experimental gill nets with meshes ranging from 1 to 4 inches, dynamite, rotenone, and electric shocks. In waters less than 4 feet deep, along the shore, I used "Common Sense" seines, a push seine, bag seine, and dip net. In Sandusky Bay the fishermen employed haul seines. See table 1 for methods of collection for each month and year and table 2 for methods of collection for each locality.

Data Recorded for Individual Fish

All fish lengths in this paper are standard lengths, in millimeters. Lengths of small fish were determined with the aid of a pair of dividers. Larger fish were measured on a measuring board. Most of the measurements were taken shortly after the fish were caught. When the sample was large, some of the fish were kept temporarily (1 to 2 days) in 10 percent formalin. Preservation in formalin for a week resulted in no perceptible

TABLE 1.—*Number of gizzard shad collected in 1952–55 by methods, year, and month*

[Number of samples in parentheses]

Year and month	Method of collection										Total
	Small-mesh seine[1]	Haul seine	Picked up dead	Experimental gill net	4- or 5-inch mesh gill net	Commercial trap net	Otter trawl	Dynamite	Rotenone	Electric shocking	
1952:											
July	125 (5)										125 (5)
Aug	27 (3)				247 (1)						274 (4)
Sept	9 (2)					17 (2)					26 (4)
Oct	1 (1)										1 (1)
Nov	183 (7)					77 (1)					260 (8)
Dec	92 (6)						390 (2)				482 (8)
1953:											
Jan	24 (3)						7 (1)				31 (4)
Feb			27 (5)								27 (5)
Mar			2 (1)								2 (1)
Apr					1 (1)	324 (17)					325 (18)
May		115 (1)				129 (6)					244 (7)
June	81 (3)	158 (2)									239 (5)
July	1,456 (11)	64 (3)									1,520 (14)
Aug	836 (10)	34 (4)		543 (2)						67 (3)	1,480 (19)
Sept	26 (2)					1,195 (6)					1,221 (8)
Oct	4 (1)			158 (2)		725 (10)					897 (13)
Nov					13 (4)	1,762 (9)					1,775 (13)
Dec					21 (6)	403 (1)	2 (1)				426 (8)
1954:											
Jan			63 (1)		46 (9)						109 (10)
Feb			44 (1)		242 (16)						286 (17)
Mar					20 (7)						20 (7)
Apr					29 (8)	39 (8)					68 (16)
May					18 (7)	63 (11)					81 (18)
June	268 (2)				427 (21)	713 (14)					1,408 (37)
July	143 (9)				227 (8)	540 (16)			650 (2)		1,560 (35)
Aug				94 (2)	120 (7)	77 (2)		7,428 (2)	943 (2)		8,662 (15)
Sept								876 (1)			876 (1)
Oct				132 (1)							132 (1)
Nov											
Dec											
1955:											
Jan					3 (1)						3 (1)
Feb					19 (8)						19 (8)
Mar					2 (1)	2 (1)					4 (2)
Apr					161 (5)	148 (9)					309 (14)
May					6 (3)	204 (12)					210 (15)
June					459 (44)	284 (6)					743 (50)
Total	3,275 (65)	371 (10)	136 (8)	927 (7)	2,061 (157)	6,702 (131)	399 (4)	8,304 (3)	1,593 (4)	67 (3)	23,835 (392)

[1] Of various types mentioned in text.

TABLE 2.—*Gizzard shad collected in 1952–55 by method and locality*

[Number of samples in parentheses]

Locality	Method of collection										Total
	Small-mesh seine[1]	Haul seine	Picked up dead	Experimental gill net	4- or 5-inch-mesh gill net	Commercial trap net	Otter trawl	Dynamite	Rotenone	Electric shocking	
Fishery Bay (South Bass Island, Ohio)	2,350 (38)		126 (7)	927 (7)	1,558 (134)			8,304 (3)	1,593 (4)	67 (3)	14,925 (196)
Bass Islands, Ohio (except Fishery Bay)	27 (1)				316 (21)	6,702 (131)	399 (4)				7,444 (157)
Sandusky Bay, Ohio	76 (4)	371 (10)									447 (14)
Portage River, Ohio	116 (7)										116 (7)
Sandusky River, Ohio	233 (4)										233 (4)
Kelleys Island, Ohio	28 (2)										28 (2)
Pelee Island, Ontario	218 (2)										218 (2)
Green Creek Marsh, Ohio	46 (1)										46 (1)
East Harbor, Ohio	74 (1)										74 (1)
Colchester, Ontario	26 (1)										26 (1)
Long Point, Mich	44 (1)										44 (1)
Point Pelee, Ontario	10 (1)										10 (1)
Avon Lake, Ohio					187 (2)						187 (2)
Mouse Island, Ohio	4 (1)										4 (1)
Maumee Bay, Ohio	23 (1)										23 (1)
Vermilion, Ohio			10 (1)								10 (1)
Total	3,275 (65)	371 (10)	136 (8)	927 (7)	2,061 (157)	6,702 (131)	399 (4)	8,304 (3)	1,593 (4)	67 (3)	23,835 (392)

[1] Of various types mentioned in text.

change in length; and the loss in weight was about 1 percent.

The relation of total length to standard length was obtained by fitting a line by means of least squares to the length measurements. The regression equation was $L_t=4.9+1.23\ L_s$, where L_t is total length and L_s is standard length.

For the determination of age, three or more scales were removed from every gizzard shad longer than 100 mm. Among the smaller shad, scales were taken from random samples of fish from each collection. The scales were placed on a glass slide immediately after removal from the fish, and their annuli counted with the aid of a dissecting microscope. The ages assigned were in terms of the number of annuli. Since the age designation changes on January 1, a fish captured between this date and the actual time of annulus formation was credited with a "virtual annulus" at the edge of the scale (Hile, 1948).

The scales employed in the study of the body-scale relation and for the calculation of growth were removed from a "key area." Since gizzard shad lose their scales readily, a "key scale" frequently would have been missing or regenerated. Use of a key area eliminated discarding shad which lacked the one particular key scale. The key area is on the left side of the fish, just dorsal to a midlateral line and midway between the posterior edge of the operculum and the origin of the dorsal fin. A dozen or so scales from this area were placed in a scale envelope on which was recorded the information pertinent to the fish.

Three nonregenerated scales were taken at random from these key-area scales. For study, they were either impressed on strips of plastic by a cold roller press (Smith, 1954) or mounted dry on glass slides.

The scale measurements were obtained from scale images projected by a microprojection apparatus of the type described by Van Oosten, Deason, and Jobes (1934).

Computations of growth from scale measurements were made nomographically.

Weights are expressed in grams. The largest fish were measured to the nearest gram, fish between 100 and 200 mm. in standard length to the nearest 0.5 g. and those smaller than 100 mm. to the nearest 0.1 g. In catches of large numbers of gizzard shad smaller than 50 mm., those of equal length were weighed en masse and the average weight assigned to each member. Fish preserved for a few days in formalin were sometimes used. Some fish were not weighed when collections were large. Gonads—only from freshly caught shad—were weighed to the nearest 0.01 g.

Ovaries from potential spawners caught in May, June, and July were used for egg counts. From one of the weighed ovaries a small transverse section (1 to 2 g.) was removed and weighed on an analytical balance, its content of current-season eggs counted, and the number of eggs in the entire ovary calculated.

Histological preparations were made of the ovaries of some fish captured in different seasons for studies of oögenesis and ovarian growth and development.

Sex was always determined by dissection except for those fish from which eggs or milt were flowing during the spawning season. When possible, sex was determined for all fish longer than 120 mm. Maturity of males could not be determined in the absence of flowing milt.

SCALE OF THE GIZZARD SHAD

Description of the Scale

The gizzard shad has cycloid scales whose annual growth zones contain many circuli. The relatively closer juxtaposition of the circuli in the first growth zone than in the succeeding zones contributes a darker appearance to this inner portion of the scale. The closely set circuli of this zone are gently arched and, save for those formed earliest, do not curve enough at their ends to reach the transverse groove that separates the anterior and posterior fields but terminate in the lateral fields. This pattern is followed by the circuli of each succeeding growth zone; i.e., the earliest circuli reach the transverse groove, while those produced later terminate laterally. The first circulus of the second growth zone is closely juxtaposed to the last circulus of the preceding zone in the anterior field, cuts across the paths of the later first-zone circuli at their terminations in the lateral fields, and intersects the transverse groove. Thus, it forms roughly a semicircle around the first growth zone. The junction between the first and second growth zones (fig. 2) illustrates one type of demarcation line in the gizzard shad scale. The first annulus of all shad scales examined was of this type. Since this annulus normally is evident only in the lateral fields where the termination of the circuli of the first zone is "cut across" by the circuli of the second zone, it may escape notice under low magnification.

A second type of demarcation line, characterized by a narrow band devoid of clear-cut circuli, normally is found between all growth zones beyond the first. Here, too, the earlier circuli of the more recent zone cut across the paths of the later circuli of the preceding zone in the lateral fields. This type of annulus is clearly evident under low magnification (fig. 3).

Further study is required, but on the basis of my observations I suggest that this second type of annulus is a combination spawning mark and annulus. It is found only on the scales of fish of spawning age. The prominence of this annulus and its possession of a few fragmentary circuli indicate not only a cessation and resumption of growth, but also a period of either poor circulus formation or even of limited scale resorption. Such a period is not indicated by the first annulus. Annulus formation and spawning take place at about the same time (see next section on time of annulus formation). Although no direct causative relation between spawning and annulus formation has been demonstrated, the period of disturbed circulus formation may well be the result of rapid prespawning gonad growth. A few gizzard shad do not spawn during their third year of life (near the start of which the second annulus is formed). These fish may provide the scales on which the second annulus resembles the normal first annulus closely. This type of annulus (fig. 4) lacks the narrow band of fragmentary circuli which makes the usual second and succeeding annuli so conspicuous.

FIGURE 2.—The first annulus of a gizzard shad scale.

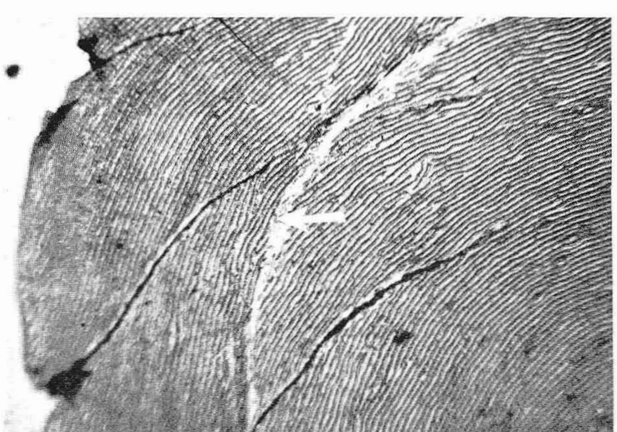

FIGURE 3.—The second annulus of a gizzard shad scale, with clear line between second and third growth zones.

FIGURE 4.—Second annulus of a gizzard shad scale resembling typical first annulus.

Further evidence on the possible effect of spawning on scale structure comes from gizzard shad that show an accessory check between the first and second annuli of their scales (fig. 5); in fact, all accessory checks found were in this position. Fish with this check may be the few shad which spawn during their second year of life. Because the first annulus is already present by the first of June, whereas any precocious second-year spawning occurs in late July—or later in the year (see section on spawning season)—the effect of this late spawning, if it is to be shown by the scale, would have to appear beyond the first annulus.

FIGURE 5.—An accessory check on a gizzard shad scale.

Time of Annulus Formation

No new annuli were observed on the scales of any age group of gizzard shad collected in the lake prior to the second quarter of May (table 3). Data for individual days in this second quarter indicated that two of the five males and eight of the nine females of age-group I, taken in the open lake on May 15, had already formed their first annulus. Only one other of the I-group fish, a female captured on May 12, 1955, collected in this quarter had the new annulus. No fish of this age group exhibited annuli in the small collections of May 16–23. (All of the 48 male and 56 female I-group fish caught in Sandusky Bay on May 22, 1953, had their new annulus—data not given in table.) All I-group shad collected after May, however, had completed the new annulus. The new annulus of the II-group fish began to appear in the first quarter of June and the year-mark was present in all of these fish by the first quarter of July. Shad older than the II-group seem to have formed the new annulus about a week later; data for these higher ages, however, are meager. The time of annulus formation, as judged from examination of scales, is in general agreement with the time of resumption of growth in length as indicated by changes in the length of fish (see fig. 8).

Once annulus formation had started, the percentage of females having the new annulus was greater than that of the males until all fish of both sexes had new annuli. On the whole, the female gizzard shad seems to form the annulus as much as a week earlier than the male.

Among the II-group shad, neither length nor weight of either sex was a determining factor in time of annulus formation (a similar study was not made of other age groups). A comparison (made only for June) of the II-group female gizzard shad which had not spawned with those which were spent demonstrated that the percentage of fish having the new annulus was about the same in both groups. Hence, we may assume that the act of spawning neither hastened nor retarded the formation of the new annulus. It may not be concluded, however, that the gonad development which ultimately results in spawning has no effect on the structural appearance of the developing annulus or upon the initiation of a check. Probable evidence of the effect of spawning is seen in the accessory check found between the first and second annuli in the scales of some shad (see previous section on description of the scale).

Validity of the Annulus as a Year-Mark

Lagler and Applegate (1943) and Lagler and Van Meter (1950) demonstrated that the annulus is a true year-mark on scales of gizzard shad in Indiana and Illinois. The following data on shad in Lake Erie add support to the belief that annuli

TABLE 3.—*Percentage of gizzard shad having a new annulus in May, June, and July*

[Combined collections of 1953–55; lake specimens only. Number of fish in parentheses]

Age and sex	Periods in May				Periods in June				Periods in July			
	1–8	9–15	16–23	24–31	1–8	9–15	16–23	24–30	1–8	9–15	16–23	24–31
I-group:												
Male	0.0 (51)	9.1 (22)	0.0 (4)	----------	100.0 (10)	----------	100.0 (83)	100.0 (18)	100.0 (50)	100.0 (1)	100.0 (55)	100.0 (21)
Female	.0 (74)	23.7 (38)	.0 (1)	----------	100.0 (8)	----------	100.0 (37)	100.0 (19)	100.0 (75)	100.0 (3)	100.0 (71)	100.0 (20)
II-group:												
Male	.0 (23)	.0 (37)	.0 (23)	0.0 (4)	24.2 (120)	8.4 (166)	52.0 (246)	84.9 (86)	100.0 (29)	100.0 (7)	100.0 (27)	100.0 (2)
Female	.0 (34)	.0 (48)	.0 (37)	----------	32.8 (67)	30.7 (75)	66.4 (125)	96.9 (97)	100.0 (47)	100.0 (13)	100.0 (16)	100.0 (5)
III–VI-group:												
Male	.0 (3)	----------	.0 (6)	.0 (1)	.0 (16)	.0 (26)	.0 (24)	50.0 (2)	75.0 (4)	100.0 (1)	.0 (1)	----------
Female	.0 (3)	.0 (5)	.0 (4)	----------	.0 (5)	.0 (8)	16.1 (31	75.0 (32)	100.0 (26)	95.2 (21)	----------	----------

are valid indicators of age. (Later sections include considerable supporting data on certain of the points.)

1. Gizzard shad known to be young of the year had no annuli on their scales.

2. The scales of these young shad captured in the fall, winter, and early spring showed no annulus at the edge, whereas those taken later exhibited increasing percentages with an annulus until all possessed them.

3. The distance between the last annulus and the scale edge increased through the growing season.

4. Presumed age groups as indicated by modes in length-frequency groupings of shad agreed with groupings based on the number of annuli.

5. The calculated lengths for particular years of life among the age groups of the same and different years of collection agreed with estimates of length from modes of frequency distribution.

Body-Scale Relation

The relation between fish length and scale length in gizzard shad was determined from the "key-area" scales of some 700 fish, ranging in standard length from 43 to 390 mm. A test plotting of the length of the anterior radius (center of focus to anterior edge) of the scale against the standard length of the fish indicated the relation to be linear. The regression line, $L=22.1+44.25\ S$, was fitted by least squares; L=standard length of the fish in mm. and S=anterior radius of the scale in mm. Fish captured in every month and including age-groups I through VI of both sexes are represented in this equation. Studies of the body-scale relation for each sex, for each age group, and during each month revealed no appreciable variation from the general equation.

The empirically derived body-scale equation was the basis for construction of a nomograph for the calculation of growth from scale measurements.

AGE COMPOSITION

Seasonal movements, segregation by size and possibly by maturity, and selectivity of collecting methods complicated the problem of sampling for age composition. The very young gizzard shad of western Lake Erie were found in midsummer close to shore, usually in shallow water. Collecting representative samples of these fish presented difficulties. Capture of the very youngest required the use of dip nets which, of course, the larger fish eluded. As the season progressed and the fish grew larger, Common Sense seines and bag seines were used, but this gear permitted the very smallest fish to pass through the meshes while many of the larger ones escaped capture by their agility and speed. The use of rotenone was selective for the very young shad that could not swim through the poisoned water rapidly enough to avoid being overcome. (Rotenone was used in small areas in the lake with no provisions for holding the fish within the sampling area or for preventing dissipation of the poison into the surrounding waters.) Electrocuting, on the other hand, was selective for the larger shad—the very young ones were unaffected. Finally, I used dynamite. This method proved most successful because fish of all sizes and ages surfaced within the radius of its effectiveness.

As the young gizzard shad become larger (and older) they move into deeper water offshore. By October, the Common Sense seine, which must be fished inshore, will capture some O-group shad but no I-group or older ones; hence, its catches yielded no data on age composition. The gill net captures large O-group shad and also all the older age groups in October, but many smaller O-group shad must pass through the net. Because of these sampling problems, estimates of age composition are unreliable among the 4- to 8-inch shad. Only a few fish of these sizes were captured by experimental gill nets whose meshes ranged from 1 to 4 inches, stretched measure.

Except during the spawning season, gizzard shad older than age-group III were rarely found in the shallower waters. This preference for the deeper water seemed to increase with age.

In view of the segregation by size and the seasonal changes of distribution, small-scale methods of collection could not provide suitably accurate data on age composition. I lacked especially the means to compare data on the 1- to 4-inch group from the shallow waters with records for larger shad from the deeper waters.

Seasonal Changes of Age Composition

Because of the difficulties just outlined, O-group gizzard shad caught by any means other than by trap nets and 4-inch-mesh gill nets have been excluded from this section. The O-group shad in our collection area appear in June, rise to greatest abundance about late July, and diminish in numbers thereafter. Greatest losses occur, presumably, as a result of predation and migration from the collection area.

Although O-group gizzard shad were taken in greatest numbers in late July, none of them had become large enough to be caught by the gill nets and trap nets until August. Subsequently, the size of the collections of the O-group coming into this catchable size range increased regularly until they reached peak abundance toward the end of the calendar year (table 4). They were the dominant age group among fish taken by these nets from August to the end of the year. From January to August of the next year, contrary to expectation, these fish, as the I group, were not dominant in the catch of gill nets and trap nets. Over this period the II-group fish dominated the catches. After August, however, the I group became more plentiful than the older groups and maintained that abundance thereafter.

The scarcity of I-group gizzard shad in the gill net and trap net samples from January to August cannot be fully explained. When all the fish captured in January–July are considered (whether they were obtained by dynamite, rotenone, electrocution—data not tabulated here), then the I group is the dominant group in the collecting area in all the early months except June and July. The June collection especially is noteworthy—the I group was very poorly represented in samples from both the lake and Fishery Bay—especially in the bay where only 4 I-group shad were collected along with 820 II-group fish.

It is noteworthy that the II-group and older shad were taken principally in April through July. Only during the spawning season (June–July) was I able to capture the VI-group shad, which were the oldest in the samples. The August–September samples were dominated overwhelmingly by age group I (89.0 to 98.8 percent). The II group made up 1.2 to 10.6 percent, and only four older fish were taken in the 5 months.

Sampling difficulties, as previously described, prohibited any detailed consideration of fluctuations of year-class strength; however, the 1952 year class apparently was one of unusual abundance. In random samples from commercial trap nets this year class made up 85 percent of the total as age group I, 71 percent as age group II, and 11 percent as age group III.

TABLE 4.—*Age composition of gizzard shad taken by trap nets and 4-inch-mesh gill nets, Lake Erie, 1954*

[Percentages of fish in age-groups I-VI given in parentheses—the O-group fish were not considered in the computation of percentages or average age]

Month	Age group O	I	II	III	IV	V	VI	Total and average age [1]
Jan	([2])	4	44	1				49
		(8.2)	(89.8)	(2.0)				1.94
Feb	([2])	12	56	3	2			73
		(16.5)	(76.7)	(4.1)	(2.7)			1.93
Mar	([2])	2	16	5				23
		(8.7)	(69.6)	(21.7)				2.13
Apr	([2])	316	330	36	7	1		690
		(45.8)	(47.8)	(5.2)	(1.0)	(0.1)		1.62
May	([2])	190	187	16	5	1		399
		(47.6)	(46.9)	(4.0)	(1.3)	(.3)		1.60
June	([2])	44	1,656	125	14	2	2	1,843
		(2.4)	(89.9)	(6.8)	(0.8)	(.1)	(0.1)	2.07
July	([2])	287	446	29	4	1	1	768
		(37.4)	(58.1)	(3.8)	(.5)	(.1)	(.1)	1.68
Aug	256	226	27	1				254
		(89.0)	(10.6)	(0.4)				1.11
Sept	899	304	7	1	1			313
		(97.0)	(2.2)	(.4)	(.4)			1.04
Oct	667	221	15	1				237
		(93.2)	(6.3)	(.5)				1.07
Nov	1,686	164	2					166
		(98.8)	(1.2)					1.01
Dec	320	97	5					102
		(95.1)	(4.9)					1.05

[1] Average number of annuli.
[2] Young of the year first became available to the nets in August.

Survival Rate

Although the records (table 4) do not give a fully satisfactory idea of the age composition of the gizzard shad stock, the collections made in April–July probably permit fairly reliable inference as to the ratios between the numbers in successive age groups for II-group and older shad, since these mature fish seem to constitute a homogeneous group during this period. Collections made from August to December are probably reasonably reliable for determining the ratio of the I-group to the II-group shad. From these two sets of data, I have estimated the survival rate of shad from one age group to the next higher one (table 5).

An estimate (not given in table 5) was made also of the survival of gizzard shad from egg deposition to age-group I. The first step was the calculation, from data on sex ratio (table 15) and fecundity (table 18), of the probable number of eggs deposited by the gizzard shad of age-group II and older. The females of the 6,049 fish (total of the II-group and older of the right-hand column of table 5) were thus estimated to have deposited 926 million eggs. If the 100,000 I-group fish of table 5 are held to be the survivors of this number of eggs (it is assumed that the population is relatively stable), survival from the egg to age-group I is determined as 0.011 percent. This estimate is beset with many uncertainties. It assumes, for example, that the determination of the number of I-group individuals from the ratio of numbers of fish in age-groups I and II in August–November samples was accurate; that year-to-year differences of stock were small enough to justify the pooling of data in the preparation of table 4; that the samples that contributed to table 5 were not unduly biased by gear selection or segregation by size or sex. Even if we granted the survival of 0.011 percent from egg to I-group a wide margin of error, however, the extremely low value still indicates an enormous mortality.

The extraordinarily low survival of the gizzard shad from eggs to the I-group fish probably results from heavy egg and larval mortality, predation, and (in late fall and early winter) buffeting during storms as well as rapid variations in water temperature. When they become the I-group fish, they are usually too large to be eaten by most predatory fish, but they are susceptible to storms and temperature changes that are greatest in waters relatively close to shore where this age group is usually found. As the shad become older, the survival rates improve, probably because the fish tend to remain in the deeper waters where they are less subjected to climatic disturbances.

The oldest gizzard shad that I collected from the western end of Lake Erie in 1952–55 were three of age-group VI (seventh year of life). Patriarche (1953) reported X-group gizzard shad from Lake Wappapello, Mo.

LENGTH-WEIGHT RELATION

General Relation

The mathematical relation between length and weight of gizzard shad captured in western Lake Erie in 1952–55 was determined by fitting the equation $W=cL^n$ to the average empirical lengths and weights of fish in each 10-mm. length interval. The length-weight relation was investigated for each month in which sufficiently large samples were taken. Between mid-1952 and mid-1955 there were 25 such monthly samples. At least one equation was determined for each of the 12 months (for some months adequate samples were acquired in each of the 2 or 3 years—hence, two or three equations). For a month having more than one equation, length and weight data were obtained by each equation, and from these an average monthly length-weight relation was determined. In like manner a "general" length-weight equation was determined from the data calculated by the monthly equations. The sexes were combined for all monthly equations. The general equation was $\log W = -4.81765 + 3.07053 \log L$, where W is the weight in grams and L is the standard length in millimeters.

TABLE 5.—*Survival of gizzard shad from one age group to the next higher one*

[The figures in the first column, body of table, obtained from table 4]

Period of capture and age group	Number of fish	Survivors from 100,000 I group
August–December		
I	1,012	100,000
II	56	5,534
April–July		
II	2,619	5,534
III	206	435
IV	30	63
V	5	11
VI	3	6

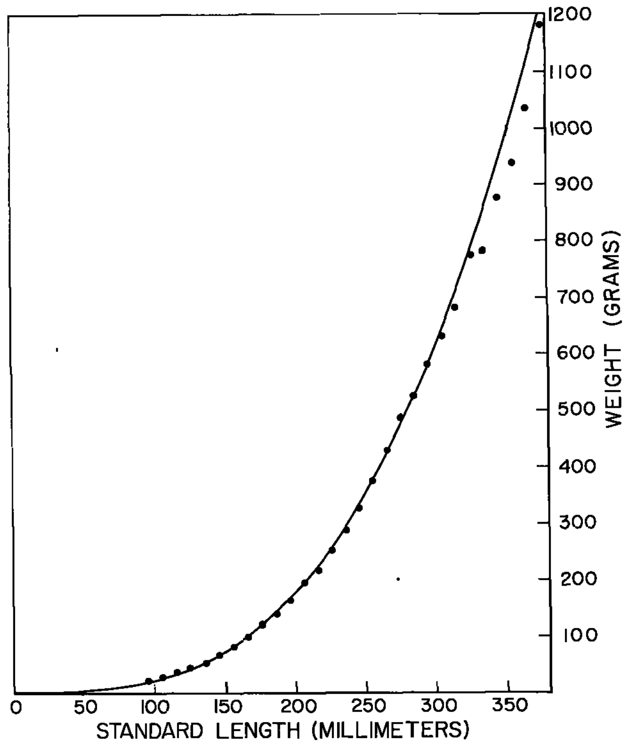

FIGURE 6.—Length-weight relation of gizzard shad in western Lake Erie. The curve is a graph of the general length-weight equation; the data represent the mean empirical values, derived as explained in the text, for the combined collections of 1952–55.

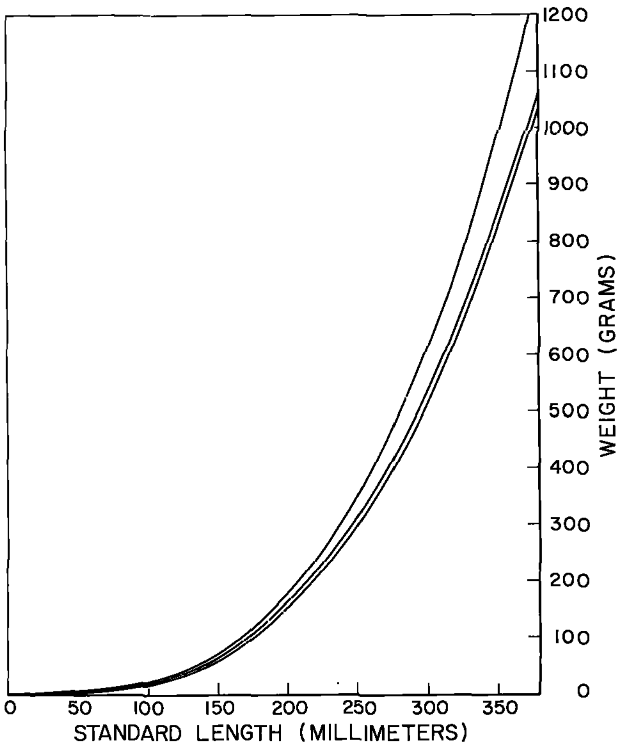

FIGURE 7.—Length-weight curves for gizzard shad from Lake Erie, Missouri, and Illinois. Left curve, Lake Erie; middle curve, Missouri; right curve, Illinois.

Empirical weights and the weights calculated by the general length-weight equation (table 6; fig. 6) agreed well in view of the heterogeneous nature of the materials (records of weight were combined without regard to season, year, sex, maturity, or method of capture). Largest disagreements in measurements concerned the longest fish.

Patriarche and Lowry (1953) determined the length-weight equation to be log $W=-2.2071+2.9812 \log L$ for gizzard shad in the Black River Basin of Missouri. Lagler and Van Meter (1950) reported the equation to be log $W=-2.2789+3.034 \log L$ for shad in Illinois. In both equations, the units are weight in ounces and total length in inches. The curves based on these equations show the Lake Erie shad to be heavier for corresponding lengths than those in Missouri and Illinois (fig. 7).

The weights of male and female gizzard shad were closely similar except in June and July, when the females were consistently heavier than males of corresponding length. This difference frequently has been explained on the basis that the female's ovaries are heavy with eggs soon to be spawned. Although the weight of the ovaries contributes strongly to the heavier total weight of the female gizzard shad, it does not explain it entirely. To investigate this point, the body weight (exclusive of gonad weight) of both sexes should be compared. Unfortunately, I had taken relatively few gonad weights of males—and these over a period of several months which cut across the seasonal changes of weight. However, since the testis weight averaged 1.4 percent of the body weight for these males, I thought I could eliminate the greater part of the weight advantage offered by the ovary by adjusting the female shad's weight to include ovaries weighing only 1 percent of her body weight.

TABLE 6.—*Empirical weights and weights calculated by the general length-weight equation for gizzard shad in western Lake Erie, 1952–55*

Standard length	Weight		Standard length	Weight	
	Empirical	Calculated		Empirical	Calculated
Millimeters	*Grams*	*Grams*	*Millimeters*	*Grams*	*Grams*
20	0.08	0.15	226	251	257
30	.5	.5	236	289	295
40	1.3	1.3	246	328	333
96	20	19	256	373	376
106	26	25	266	428	424
116	35	33	276	484	473
125	43	42	285	525	526
136	54	54	295	581	583
146	67	67	305	629	645
156	82	82	315	680	713
166	99	99	326	776	794
176	118	119	335	781	864
186	138	141	344	876	938
196	161	165	355	937	1,032
206	194	193	365	1,034	1,118
215	215	222	377	1,179	1,234

The adjusted weights of these fish were still greater than those of male shad of corresponding length (table 7). The lesser weight of males may result from their greater activity during the spawning season.

Effect of State of Ovaries on Weight

The study of the effect of the state of development of the ovaries on the weight of the fish was based on records for three categories of fish caught in June 1955: will not spawn, will spawn, and spent.

The gizzard shad that would not have spawned were the heaviest (table 8). The average weight of females which would have spawned was 96 percent of that of the shad which would not have spawned. It appears that the production of mature eggs for spawning reduces the fish's total weight—possibly because some food is stored as

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TABLE 7.—*Comparison of weights of male shad at 20-mm. intervals with those of females whose weights have been adjusted to include ovaries of only 1 percent of their body weight*

[Based on June 1955 collection]

Standard length	Weight	
	Males	Females
Millimeters	*Grams*	*Grams*
200	158	189
220	210	244
240	271	309
260	344	383
280	428	467
300	525	563
320	636	669
340	760	788
360	900	919

oil in the eggs rather than as the heavier protein of flesh. The spent fish weighed the least. Their average weight was 85 percent of that of the fish which would not have spawned during the current season. The average percentage loss of weight of mature females at spawning increased with length of fish and averaged 10.7 percent.

Seasonal Differences in the Weight of Fish of a Given Length

The weight of gizzard shad of a given length varies from season to season, and this seasonal variation is similar from year to year. The nature of the seasonal changes (table 9) appears from the average monthly length-weight data. In June and July, when weights of the sexes differed appreciably, the males and females were treated both separately and combined; in other months they were combined.

Gizzard shad attained their greatest weight in August–October, after which the weight declined slowly and irregularly, reaching a low for the combined sexes about May–June. (Interpretations are handicapped by differences of slope in the monthly logarithmic lines.) During the next 2 months, the weights increased rapidly. The weight of the female was least in May (not shown in table 9), and an increase was obvious in June, but that of the male reached the lowest point in June.

Studies of the gut contents indicate that gizzard shad consume little food in winter and early spring. During this period they subsist largely on energy stored in the body tissues. Because metabolic rates are low in winter, decrease of the body weight is slight. As the water temperature rises in early spring, the metabolic rate of the fish increases more rapidly than the rate of food intake and the body weight decreases more rapidly. This process gains momentum with the progression of spring until about May–June when the lowest body weight is attained apparently just before the renewed feeding begins to meet the energy requirements of the fish. The occurrence of peak weight, in August–October, undoubtedly is directly related to feeding.

Continued loss of weight in June among the males can be attributed to their spawning activities.

TABLE 8.—*Weights of three groupings of female gizzard shad of different ovarian development, June 1955*

Standard length	Weight of females in category			Loss at spawning
	Would not have spawned	Would have spawned	Spent	
Millimeters	*Grams*	*Grams*	*Grams*	*Percent*
280	510	484	473	2.3
300	610	583	543	6.9
320	722	694	617	11.1
340	846	818	695	15.0
360	982	954	779	18.3

TABLE 9.—*Monthly variations of weight of gizzard shad as determined from the monthly length-weight equations*

WEIGHT

Standard length	January	February	March	April	May	June			July			August	September	October	November	December
						Males	Females	Combined sexes	Males	Females	Combined sexes					
Millimeters	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*
200	177	170	179	157	158	161	192	177	186	183	185	198	193	189	181	183
220	240	228	240	215	212	213	249	231	241	242	242	264	256	256	241	245
240	317	298	314	287	277	275	315	295	304	313	309	342	330	336	313	320
260	410	381	402	374	355	348	391	370	377	397	387	435	419	433	398	409
280	519	479	506	478	446	433	478	455	460	494	478	543	521	547	497	514
300	646	593	626	600	551	531	575	553	553	606	580	668	639	680	612	635
320	794	723	764	743	673	642	685	663	658	734	696	810	773	834	742	774
340	963	872	922	907	811	767	807	787	774	878	826	972	924	1,010	890	933
360	1,156	1,039	1,100	1,096	967	908	942	924	902	1,040	971	1,153	1,094	1,209	1,056	1,111

TABLE 10.—*Annual differences of weights of gizzard shad in 1952–55*

[Years compared by pairs; data limited to months for which records are available for both members of the pair]

Standard length	Weights by years									
	1952	1953	1952	1954	1953	1954	1953	1955	1954	1955
Millimeters	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*
200	190	186	197	189	172	174	154	169	165	172
220	253	249	264	252	231	237	207	226	223	229
240	330	326	345	326	303	312	272	296	293	297
260	421	416	442	415	389	403	348	379	378	378
280	525	523	555	517	490	510	440	476	478	472
300	650	645	686	636	608	636	546	590	595	581
320	790	787	837	771	744	781	668	720	730	705
340	950	948	1,008	924	898	948	807	869	885	846
360	1,146	1,130	1,204	1,096	1,078	1,138	966	1,036	1,061	1,005
Rating of years	1952>1953		1952>1954		1953<1954		1953<1955		1954>1955	
Months used	Aug., Nov., Dec.		Aug.		Jan., Feb., Apr., May, Aug., Oct.		Feb., Apr., May		Feb., Apr., May, June	

Annual Differences in Weight

The study of the annual differences in the length-weight relation of gizzard shad in 1952–55 was based on data for only those months during which adequate collections were made in at least two of these years. As was brought out in the previous section, the weight of shad varies with the season. Since samples were not adequate for determination of length-weight relations for every month of each year, the use of yearly data would result in a bias in favor of the year during which the specimens were obtained in the months of greatest weight. Consquently, the paired comparisons for 1952–55 were based only on data from months common to both years being compared (table 10).

Shad were heaviest in 1952 and lightest in 1953. The rating of years ran: 1952>1954>1955>1953.

LENGTHS AND WEIGHTS OF AGE GROUPS

The average size of the members of an age group varies with time of capture within the year along clearly seasonal lines. The monthly average lengths of shad show little growth in early spring, rapid growth in summer and early fall, and apparently a cessation of growth in winter for both sexes and all age groups (table 11). The course of growth becomes more apparent when portrayed graphically (fig. 8). After about June of their second year of life female shad were rather consistently longer than males of corresponding age.

The average monthly weights of shad showed, in general, a gradual decrease from the first of the year until June (table 11; fig. 9). This decline

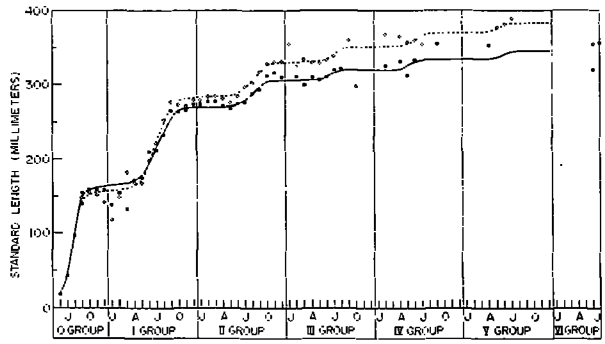

FIGURE 8.—Lengths of gizzard shad at capture in each month by age and sex. Dots are empirical averages of standard length. Open dots represent females; solid dots, males. Curves were drawn by inspection.

was followed by a rapid rise in late summer and fall. Seasonal variation of the length-weight relations (see earlier section) contributed to these changes. The female shad were heavier than males after about June of their second year of life.

The average monthly lengths of the O-group shad warrant special comment. Because some gizzard shad can be found in the spawning state in western Lake Erie from early June to mid-July (see section on length of spawning season), every sample of young shad collected usually contained fish hatched over a period of time, the extremes of which often differed in age by as much as a month or more. The successive collections continually yielded low average changes in length because of the great percentage of the newer, smaller shad constantly added to the population. This bias was aggravated by the tendency of the larger O-group fish to move off-

TABLE 11.—*Average standard lengths and weights of gizzard shad at capture*

Month of capture	O group		I group				II group				III group				IV group				V group				VI group			
	Length	Weight	Length		Weight		Length		Weight		Length		Weight		Length		Weight		Length		Weight		Length		Weight	
			Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
	Mm.	*G.*	*Mm.*	*Mm.*	*G.*	*G.*	*Mm.*	*Mm.*	*G.*	*G.*	*Mm.*	*Mm.*	*G.*	*G.*	*Mm.*	*Mm.*	*G.*	*G.*	*Mm.*	*Mm.*	*G.*	*G.*	*Mm.*	*Mm.*	*G.*	*G.*
Jan			133	123	53	42	282	292	503	585		*356		*1,169												
Feb			*146	129	*69	48	274	283	479	539	314	*305	705	*714	*325	*368	*798	*1,253								
Mar			*133	*198	*52	*174	280	282	519	515	*298	*334	*574	*865												
Apr			165	165	85	84	269	279	406	473	308	328	631	835	*324	*364	*678	*1,072	*354		*809					
May			167	160	87	77	267	269	384	411	303	329	540	750	*312	*356	*623	*911		*378		*1,040				
June	18	0.1	195	204	158	188	272	283	396	503	310	333	592	778	333	358	691	926		*382		*1,082	*321	*355	*729	*1,114
July	38	0.7	213	218	232	249	275	294	442	572	320	338	626	854		*355		*1,008		*390		*1,350	*357		*810	
Aug	61	28	232	241	294	356	285	302	531	687	*313		*636													
Sept	119	79	258	268	408	446	*303	*317	*568	*722		*360		*1,162	*355		*897									
Oct	152	84	264	265	441	457	312	330	750	871																
Nov	152	86	261	269	424	469	*316	*330	*756	*996																
Dec	138	66	270	273	468	500	*310	*335	*816	*966																

*Asterisk indicates an average based on fewer than five fish.

shore from the sampling area and their growing ability to avoid capture. As a consequence, the sequence of these low average monthly lengths cannot be construed to indicate the rate of growth for these young shad. It was held desirable, therefore, to estimate the position of certain points and of the curve in the preparation of figure 8. No precise quantitative justification can be given for these estimates, but they were based on broad sampling experience and extensive observations on catches in inshore waters. The estimates are held surely to be superior to judgment based on the sadly biased sample records. The curve and points of figure 8 beyond age-group O are based strictly on the records of table 11. The records of monthly growth of table 12 were read from the curve of figure 8.

Gizzard shad of age-group O presumably grew most rapidly in July, August, and September and had peak growth in August. The record for I- and II-group shad indicates that growth in length of the I-group fish progresses rapidly earlier in the year than it does for the II-group. Greatest gain occurred a month earlier—in July. Growth was slight for both groups during May and for the I-group after September.

During the second year of life the male shad grew in length 57 percent as much as during the first year, and in the third year, 28 percent as much. For the female shad the second- and third-year growths were 66 percent and 34 percent, respectively, of the first-year growth.

Seasonal changes in weight resemble those in length (compare figs. 8 and 9) except that weight decreases over winter from the peak attained during the previous fall. The basis for this change was explained earlier in the section on seasonal changes in weight.

Attempts to follow seasonal growth of gizzard shad by use of tagged individuals were unsuccessful. No fish were recaptured from some 600 tagged during the winter of 1952.

CALCULATED GROWTH

Calculated Lengths of Age Groups

The dependability of calculations of length at time of annulus formation is indicated by comparison of the calculated lengths and the lengths of shad which were captured between the end of the growing season and the time of annulus formation (first and last columns of table 13). Because the annuli are the only landmarks on the scale which can be related to a somewhat definite time, and because the shad has practically the same length from the beginning of the calendar year to the time of the annulus formation, the length of a shad captured in this period should agree closely with the length calculated from an older fish to the corresponding annulus.

Agreement was close among adequately represented age groups except for the I-group shad. In the compilation of the empirical data for this group, 105 shad had to be eliminated because sex could not be determined with certainty; their average standard length was 129 mm. Had they been included, the disagreement between empirical and calculated lengths would have been less, but

TABLE 12.—*Progress of season's growth in length of gizzard shad by millimeters and percentage*

[Lengths taken from the curves of figure 8]

Period	O-group				I-group								II-group							
					Male				Female				Male				Female			
	Average length	Increment of growth	Accumulated growth	Growth during month	Average length	Increment of growth	Accumulated growth	Growth during month	Average length	Increment of growth	Accumulated growth	Growth during month	Average length	Increment of growth	Accumulated growth	Growth during month	Average length	Increment of growth	Accumulated growth	Growth during month
	Mm.	*Mm.*	*Percent*	*Percent*	*Mm.*	*Mm.*	*Percent*	*Percent*	*Mm.*	*Mm.*	*Percent*	*Percent*	*Mm.*	*Mm.*	*Percent*	*Percent*	*Mm.*	*Mm.*	*Percent*	*Percent*
Apr. 30	----	----	----	----	167	0	0	0	164	0	0	0	263	0	0	0	273	0	0	0
May 30	[1] 5	5	3	3	175	8	8	8	175	11	10	10	266	3	6	6	276	3	5	5
June 30	22	17	13	10	199	24	33	25	204	29	37	27	271	5	17	11	282	6	16	11
July 30	50	28	30	17	225	26	60	27	233	29	64	27	282	11	40	23	294	12	38	22
Aug. 30	114	64	69	39	249	24	85	25	257	24	85	21	297	15	72	32	309	15	65	27
Sept. 30	155	41	94	25	258	9	95	10	268	11	95	10	305	8	89	17	320	11	85	20
Dec. 30	165	10	100	6	263	5	100	5	273	5	100	5	310	5	100	11	328	8	100	15

[1] These fish are assumed to be about a week old. Shad hatched in the laboratory were 3.5 mm. in standard length and became 5.2 mm. long in 4 days.

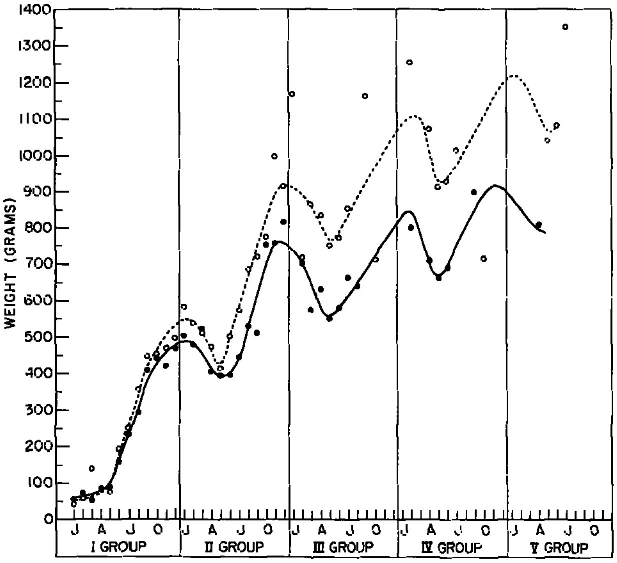

FIGURE 9.—Weights of gizzard shad at capture in each month by age and sex. Dots are empirical averages. Open dots represent females; solid dots, males. Curves were drawn by inspection.

still substantial. The principal cause of the discrepancy was probably the selective sampling of age-group I. Many of this group were too small to be caught by the gill nets and the trap nets. At the higher ages the agreement between empirical and calculated lengths was good. The lengths calculated for each year of life from progressively older shad show a similar close agreement except for the first year of life.

No year classes exhibited consistently fast or slow growth in length, nor did growth appear to have been outstandingly good or bad in any particular calendar year.

Compensatory Growth in Length

It has been observed frequently that although the larger of the young fish maintain a length advantage over the smaller ones during subsequent growth, the smaller young fish grow more rapidly during subsequent years than the larger ones and, thus, reduce progressively the original length difference.

To study this "compensatory growth" in gizzard shad, I tabulated the annual increments of growth of III-group fish, arranged by 20-mm. groupings of length at the end of the first year of life (table 14). The sexes were treated separately, and only fish caught in 1954 were used. In both sexes the annual increments generally varied inversely with first-year length; consequently, the difference in length between the shortest and the longest first-year fish diminished progressively to a minimum in the third year.

TABLE 13.—*Comparison of the average empirical standard length of gizzard shad with average length calculated for each year of life for each age group for each sex*

[Fish of the same age were combined without regard for year classes. Empirical lengths are given only for shad captured between the end of the growing season and the time of annulus formation. Number of fish in parentheses]

Sex and year of life	Average empirical length	Age group					Average calculated lengths [1]
		I	II	III	IV	V	
	Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm*	*Mm.*
Male:							
First	165 (227)	146 (76)	130 (92)	145 (34)	146 (8)	139 (2)	141
Second	273 (530)		270 (37)	282 (34)	270 (8)	270 (2)	273
Third	313 (53)			316 (5)	312 (8)	310 (2)	313
Fourth	328 (8)				348 (1)	337 (2)	343
Fifth	350 (1)					349 (1)	349
Females:							
First	162 (267)	134 (71)	139 (118)	146 (62)	144 (13)	138 (3)	140
Second	283 (489)		285 (57)	292 (62)	280 (13)	282 (3)	285
Third	335 (83)			336 (42)	333 (13)	336 (3)	335
Fourth	361 (17)				362 (6)	369 (3)	366
Fifth	383 (4)					390 (1)	390

[1] Unweighted means.

TABLE 14.—*Average annual increments of length of III-group shad of the 1954 collections arranged by 20-mm. groups of first-year calculated length*

[Second- and third-year calculated lengths given in parentheses]

Males				Females			
Number of fish	First year	Second year	Third year	Number of fish	First year	Second year	Third year
	Mm.	*Mm.*	*Mm.*		*Mm.*	*Mm.*	*Mm.*
1	96	161 (257)	49 (306)				
4	109	162 (271)	36 (307)	9	114	169 (283)	50 (333)
10	132	151 (283)	31 (314)	12	131	160 (291)	45 (336)
10	154	131 (285)	28 (313)	22	152	139 (291)	43 (334)
3	173	114 (287)	31 (318)	13	166	135 (301)	38 (339)
4	185	105 (290)	25 (315)	3	184	124 (308)	36 (344)
Difference in standard length [1]	89	33	9		70	25	11
Difference in length increments [1]		56	24			45	14

[1] Between shortest and longest first-year groups.

REPRODUCTION AND EARLY DEVELOPMENT

Size and Age at Maturity

The sex and maturity of gizzard shad were always determined by dissection except for those fish from which eggs or milt were flowing during the spawning season. Vladykov (1945) stated that the males have darker fins than the females, but I found that neither this nor any other readily discernible external characteristic indicated the sex with reasonable consistency for all age groups in all seasons. Generally, however, one might expect a shad that is relatively deep for its length to be a female. Since the time of this study, Moen (1959) sexed gizzard shad by examining the urogenital opening with a probe.

The sex of large fish was determined easily—the testes were opaque white, whereas, the ovaries were mostly semitranslucent and light yellow or pink. Sex determination was more difficult in small shad. Here, the testes were whitish and the ovaries almost colorless and translucent, but the distinction between them became less and less apparent as one examined smaller and smaller gonads. After much study (comparisons of judgments from macroscopic examination with subsequent determinations from histological sections) I could frequently distinguish the sexes macroscopically when the diameter of the gonad was only 1 mm. and readily when it attained 2 mm. The minimum standard length of fish for which sex could be determined macroscopically with confidence was about 120 mm. (4 or 5 months old), although on occasion sex could not be determined for a larger shad.

Although a fish whose milt or spawn flows during the spawning season is sexually mature, the absence of this feature does not indicate immaturity. In this situation, during the spawning season or any other time, different criteria must be employed. Histological studies of ovaries collected throughout the year have enabled me to recognize a potential spawner several months in advance of the spawning season and spent females as long as a month after spawning. Moreover, the relation of the histological characteristics of the ovary to the gross appearance of that organ made possible an estimate of maturity by gross observations. In females that will not spawn, the ovaries contain only minute, scarcely visible eggs, whereas potential spawners exhibit, in addition to the minute eggs, fair-sized ones that are clearly visible within the semitranslucent ovary several months prior to spawning. Although completely spent females have only the minute eggs that are characteristic of the ovaries of fish which will not spawn, their ovaries for a few weeks after spawning are more flaccid than those of nonspawners, the minute eggs are some little distance apart, and the interovular spaces have a more watery appearance.

The maturity of males could not be determined in the absence of flowing milt. The presence of motile sperm, obtained by lancing a testis, does not assure maturity. Males examined in January had motile sperm—even the I-group males, most of which would not spawn in the spring. Maturity in males is undoubtedly associated with structural development or physiological change which permits release of the sperm. The great scarcity of I-group males at the spawning site in May and June suggests that this release mechanism does not usually become functional in males of that age. The presence of a few of them on the spawning grounds during July may indicate that some have matured near the end of the spawning season.

In 1954, I found three mature I-group female shad. Their standard lengths were 197, 225, and 236 mm. Some 25 or 30 I-group males, 190 to 230 mm. long, also were mature. The milt and spawn produced by fish of this age were scanty. The crosssection of an ovary of a mature I-group female reveals few mature eggs (fig. 10).

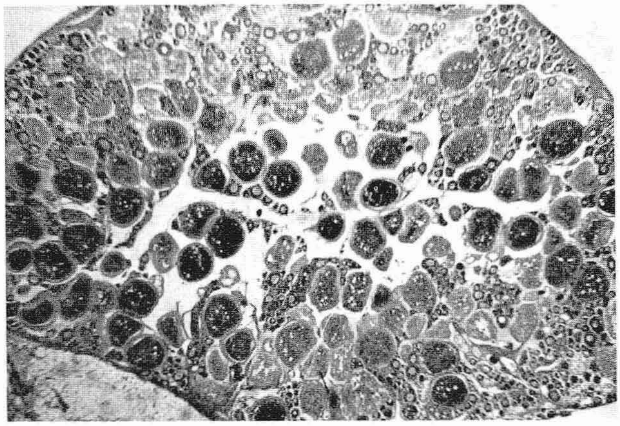

FIGURE 10.—Cross section of an ovary of a mature I-group gizzard shad showing relatively few near-mature eggs (July 6, 1954).

Invariably, these precocious fish arrived at the spawning site in July, near the end of the spawning season. They were not the largest of their age group, whose length range extended to 254 mm. at this time, but were generally above the average length. They obviously represented only a fraction of their group, but the exact percentage could not be determined because segregation according to maturity is great during the spawning season.

Most spawners were in their third year of life (II group), but not all shad of this age group spawned. The average length of the June 1954 II-group females that would have spawned (29 cm.) was 1 cm. greater than that of the shad which would not have spawned during the current year (28 cm.). Although the percentage of the female shad that matured during their third year of life could not be determined because of the segregation according to maturity, observations on gonads of shad captured throughout the year indicated that at least 80 percent of them became mature at this age in western Lake Erie. Only rarely were female shad older than the II-group immature. With few exceptions, the II-group male shad had well-developed testes. Since, however, I was unable to determine maturity in the absence of flowing milt, I could not distinguish a spent individual from one which had not spawned—in fact, could not judge from the state of the testes in any month the percentage of mature males of any age group.

TABLE 15.—*Sex ratios for gizzard shad for which both sex and age were determined monthly*

[These shad were captured in the vicinity of the Bass Islands in 1952–55]

Month and sex	Age group							Total for month
	O	I	II	III	IV	V	VI	
January:								
Male	------	7	14	------	------	------	------	21
Female	------	7	31	1	------	------	------	39
Percentage males	------	50.0	31.1	0.0	------	------	------	35.0
February:								
Male	------	8	135	5	2	------	------	150
Female	------	15	104	3	1	------	------	123
Percentage males	------	31.8	56.5	62.5	66.7	------	------	54.9
March:								
Male	------	1	5	3	------	------	------	9
Female	------	2	10	2	------	------	------	14
Percentage males	------	33.3	33.3	60.0	------	------	------	39.1
April:								
Male	------	151	156	17	3	1	------	328
Female	------	177	164	16	4	------	------	361
Percentage males	------	46.0	48.8	51.6	42.9	100.0	------	47.6
May:								
Male	------	48	90	8	4	------	------	150
Female	------	69	128	7	3	1	------	208
Percentage males	------	41.0	41.3	53.3	57.1	0.0	------	41.9
June:								
Male	------	21	913	65	4	------	1	1,004
Female	------	21	753	62	10	2	1	849
Percentage males	------	50.0	54.8	51.2	28.6	0.0	50.0	54.2
July:								
Male	------	121	172	5	------	------	1	299
Female	------	166	315	24	4	1	------	510
Percentage males	------	42.2	35.3	17.2	0.0	0.0	100.0	37.0
August:								
Male	119	104	13	1	------	------	------	237
Female	116	100	13	------	------	------	------	229
Percentage males	50.6	51.0	50.0	100.0	------	------	------	50.9
September:								
Male	410	118	4	1	1	------	------	534
Female	516	159	3	------	------	------	------	678
Percentage males	44.3	42.6	57.1	100.0	100.0	------	------	44.1
October:								
Male	319	123	9	------	------	------	------	451
Female	352	99	6	1	------	------	------	458
Percentage males	47.5	55.4	60.0	0.0	------	------	------	49.6
November:								
Male	827	73	1	------	------	------	------	901
Female	876	92	1	------	------	------	------	969
Percentage males	48.6	44.2	50.0	------	------	------	------	48.2
December:								
Male	221	37	1	------	------	------	------	259
Female	276	60	4	------	------	------	------	340
Percentage males	44.5	38.1	20.0	------	------	------	------	43.2
Total in age groups:								
Male	1,896	812	1,513	105	14	1	2	4,343
Female	2,136	967	1,532	116	22	4	1	4,778
Percentage males	47.0	45.6	49.7	47.5	38.9	20.0	66.7	47.6

Sex Ratio

The gizzard shad captured in the vicinity of the Bass Islands in 1952–55 for which sex could be determined were combined to show trends of the sex ratio by month and by age (table 15).

Only limited seasonal trends are apparent from the data on sex ratio; the month-to-month fluctuations were decidedly irregular.

Among the 10 months in which the total samples exceeded 250 fish, July stands apart because of the small percentage of males (37.0 percent). Among the other 9 months, this percentage ranged between 41.9 (May) and 54.9 (February). The percentage for all 12 months was 47.6.

The percentage of males varied little among the four younger age groups (45.6–49.7 percent males) in the combined sample for all months, but males became less numerous at the higher ages (38.6 percent in age groups IV–VI, combined).

Information on the percentage of males in samples from the shallow waters of Fishery Bay and the deeper waters of the lake gives no indication of segregation of the sexes within the lake except for age groups II and III (shad of spawning age) during June. The records for that month (table 16) suggest that males are relatively more plentiful at the spawning site than in the deeper water. The data on sex ratio on the spawning site during the spawning season are undoubtedly biased in favor of the males since their greater activity increases the likelihood of capture by the stationary fishing gear. This bias, however, does not account entirely for the large percentage of males

TABLE 16.—*Sex ratios for gizzard shad caught in the shallow waters of Fishery Bay and in the deeper waters of Lake Erie for June and for all other months combined in 1952–55*

Month and site of capture	Sex	Age group 0	I	II	III	IV	V	VI	Total
June:									
Bay	Male		5	610	47	3			665
Do	Female		6	207	16				229
Do	Percentage males		45.6	74.7	74.6	100.0			74.4
Lake	Male		16	303	18	4		1	342
Do	Female		15	546	46	10	2	1	620
Do	Percentage males		51.6	35.7	28.1	28.6	0.0	50.0	35.6
All months except June:									
Bay	Male	63	214	154	6	1			438
Do	Female	82	207	196	6	2			493
Do	Percentage males	43.4	50.8	44.0	50.0	33.3			47.0
Lake	Male	1,833	577	446	34	6	1	1	2,898
Do	Female	2,054	739	583	48	10	2		3,436
Do	Percentage males	47.2	43.8	43.3	41.5	37.5	33.3	100.0	45.8

on the spawning site; in the deeper waters the percentage of males is greater between spawnings than during the spawning season.

The sex ratios of mature shad captured in Fishery Bay and in the deeper waters of the lake within 7- or 8-day periods in May, June and July of 1954 and 1955 (table 17) indicate that the percentage of males in the population of shad captured in the bay increased during early and mid-June and reached a high in the third quarter; the females were relatively most numerous in the last quarter. Males were scarce in deeper water in June (exception, June 9–15), and with the exception of one sample (July 16–23), this scarcity continued through July. Data are few on the sex ratio in Fishery Bay in July; females predominated strongly in the single sample. The generally small percentages of males in all July samples account for the low monthly percentage for July, mentioned in the earlier description of table 15.

TABLE 17.—*Sex ratios for mature gizzard shad captured in the shallow waters of Fishery Bay and the deeper waters of Lake Erie during May, June, and July, 1954 and 1955*

Time of capture	Bay: Male	Bay: Female	Bay: Males	Lake: Male	Lake: Female	Lake: Males
	Number	*Number*	*Percent*	*Number*	*Number*	*Percent*
May:						
1–8	1	1	50.0	23	32	41.8
9–15	5	7	41.7	29	44	39.7
16–23	1	2	33.3	28	39	41.8
24–31	5	0	100.0			
1–31	12	10	45.5	80	115	41.0
June:						
1–8	135	52	72.2			
9–15	142	48	74.7	49	34	59.0
16–23	261	42	86.1	96	247	28.0
24–30	122	82	59.8	181	346	34.1
1–30	660	224	74.7	326	627	34.2
July:						
1–8	58	95	37.9	84	170	33.1
9–15				8	15	34.8
16–23				23	14	62.2
24–31				2	5	28.6
1–31	58	85	37.9	117	204	36.4

DEVELOPMENT AND MATURATION OF THE EGG

For convenience in description, the development of the egg has been divided arbitrarily into six stages (fig. 11). The following descriptions were made from ovary sections fixed in Bouin's solution and stained with hematoxylin and eosin.

Stage 1.—The young oöcyte is 10 to 20 μ in diameter and has a large nucleus with a centrally located nucleolus. The nucleolus and nuclear membrane stain darkly with the hematoxylin, while the cytoplasm and the nucleoplasm stain with eosin.

Stage 2.—The oöcyte, now 20 to 70 μ in diameter, has not yet acquired its follicle-cell envelopment. The nucleus has grown at a faster rate than the cytoplasm. This cytoplasm is now accepting some of the hematoxylin, while the ground substance of the nucleus still stains with eosin. The nucleolus, if present, is lost among the darkly staining chromatin materials which are somewhat scattered throughout the nucleus.

Stage 3.—This stage includes oöcytes which range from 0.07 mm. to 0.15 mm. in diameter. The nucleus and cytoplasm appear to have grown at the same rate from the last stage. The cytoplasm now stains darkly with hematoxylin; the nuclear sap stains pink. The dark-staining chromatin material is more plentiful and is arranged circumferentially along the periphery of the nucleus. Flat follicle cells are arranged as a single-celled layer around the oöcyte.

Stage 4.—The follicle is mostly in the 0.15-to 0.30-mm. size range in this stage. The dark-staining cytoplasm is growing more rapidly than the nucleus. As the follicle approaches the 0.30-

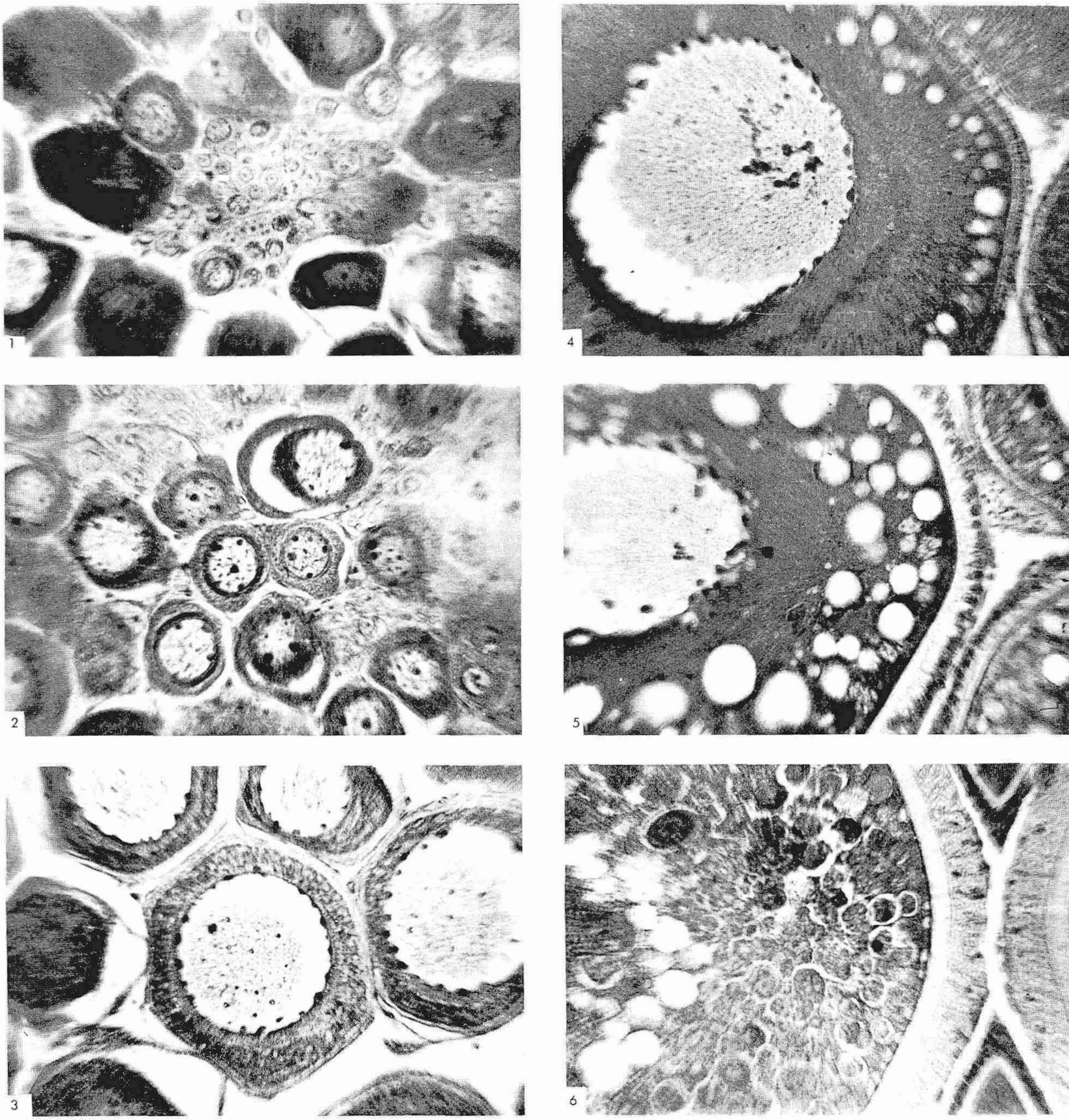

FIGURE 11.—Growth and maturation of gizzard shad eggs.

mm. size, the oöcyte's cytoplasm is stained by both hematoxylin and eosin—the resulting reddish-purple oöcyte is clearly noticeable among the bluish-purple smaller oöcytes. The nuclear membrane and chromatin material surrounding the pink-staining nucleoplasm appear fuzzy as though disintegrating. Oil globules have formed in the periphery of the cytoplasm beneath the follicle cells that have become cuboidal.

Stage 5.—In this stage the oöcyte with its envelope of follicle cells—now columnar—grows from 0.30 mm. to about 0.45 mm. The nuclear membrane has largely disintegrated, and chromatin material has all but lost its discreteness.

The peripherally formed oil globules have become larger and are moving toward the nuclear area. Small yolk granules have appeared, some of which have encroached upon the nuclear area, making this area smaller than it was in the preceding stage. These yolk granules stain mostly with eosin, while the cytoplasmic ground substance stains with both dyes. A homogeneous vitelline membrane has made its appearance between the oöcyte and its surrounding follicle layer.

Stage 6.—During this stage the follicle size is between 0.45 mm. and 0.50 mm. The nuclear membrane and chromatin material are no longer evident; the oil globules have migrated around the nuclear area and encroached upon it so that the area now is relatively small. During this migration, the yolk granules have moved away from the central area, leaving this area surrounded by oil globules. The small yolk granules of the previous stage have now become very coarse. The vitelline membrane under the single-celled follicle layer is now thick and prominent.

Up to this stage the oöcyte appeared to be isolecithal since the nucleus occupied a central position as long as it was evident and the amount of yolk compared with the size of the nucleus did not seem to be plentiful. Just prior to spawning, however, the oil globules almost completely disappear and the cell is so packed with large yolk granules that no definite nuclear region is recognizable. The tremendous amount of yolk, despite the lack of information regarding the location of the nucleus, suggests that the oöcyte now is telolecithal.

Before the egg leaves the ovary, the single-celled follicular layer ruptures and separates from the vitelline membrane. The former remains in the ovary where it gradually disintegrates. The vitelline membrane becomes greatly distended by imbibed water after the egg is spawned and water-hardened.

Most of the O-group gizzard shad already had oöcytes in Stages 1 and 2 as early as October. After they appeared, they were a constant feature in the ovary; they were most abundant in the fall in O-group fish, somewhat less abundant in older fish immediately after spawning, and least plentiful in ripe fish. In the O-group shad the oöcytes begin development so late in the season that usually they do not progress beyond Stage 2 by late fall; there is an accumulation of Stages 1 and 2. Older shad which spawned, however, showed no such accumulation, for the oöcytes that formed earliest had time to progress to later stages. Their constant presence—though they are not plentiful in near-ripe and ripe fish—indicates that one or both of the following processes must occur: these early stages are continually being formed, perhaps at varying rates; or the oöcytes formed later in the generative season—if there be one—remained more or less dormant throughout the remainder of the season—the nutrients being diverted to the earlier formed, more advanced oöcytes.

In shad which had spawned, oöcytes in Stages 3 and 4 are found in late fall and winter, but in the youngest shad (I group after January) they appear in spring.

Stages 5 and 6 usually do not appear in the I-group fish; they are present in spring in the II-group shad, and are found in spring and early summer in the older females.

SEASONAL CHANGES IN THE OVARY

The seasonal changes in the ovary of every gizzard shad are much the same after the first spawning, which occurs usually in II-group fish. Changes preliminary to first spawning follow a different course.

During fall, the oöcytes of O-group fish appear late and progress so slowly that by the time the spawning season arrives (fish are now I-group) the eggs are not mature enough to be spawned. In a few fish of this age (presumably those which hatched very early) some of the eggs become mature and are spawned late in the spawning season (fig. 10). In a few others, the eggs become mature too late to be spawned and are resorbed (fig. 12). In most of these I-group fish, however, most of the eggs have developed to Stage 4 (fig. 11), and remain at that stage until the next spawning season approaches.

For convenience, the ovarian changes of gizzard shad after their first spawning have been divided into six stages (fig. 13).

Stage A.—In late July, August, and early September, the shrunken ovary is filled with oöcytes in Stages 1, 2, and 3. The germinal epithelium extends inward from the periphery of the ovary in irregular layers. The central cavity of the saccular ovary is highly variable and is much branched. The branches extend between the layers of the germinal epithelium.

Stage B.—From late September to early November the ovary contains a greater proportion of oöcytes in Stage 3 than earlier in the season. Some oöcytes of Stage 4 are also present.

Stage C.—During winter and early spring the ovary contains some oöcytes in Stage 5, a great many in Stage 4, and decreasing numbers in the earlier stages.

Stage D.—In April, May, and early June the ovary has oöcytes mostly in Stages 5 and 6; those in Stage 6 become more and more predominant toward the close of this period. Some oöcytes in Stages 1 and 2 also are present. Those in Stages 3 and 4 are rare. The central cavity of the ovary is obliterated by the dense packing of the large oöcytes.

Stage E.—In June, the eggs in the ovary are in a stage subsequent to the last stage shown in figure 11—some are ready to be spawned. That others have left the ovary is apparent from the empty spaces and the follicular remnants. Oöcytes in Stages 1 and 2 are present—a few in Stages 5 and 6 may still be found.

Stage F.—Immediately after spawning and perhaps for a week or two later the ovary contains remnants of the old follicular layers. The oöcytes present are mostly in Stages 1 and 2, but some have already reached Stage 3.

The seasonal progression of ovarian change by no means proceeds at the same rate in all gizzard shad. The figures represent the situation for most shad in western Lake Erie. In some of the fish the stages are months in advance of those given in the figure; in others, they are months tardy. Nevertheless, differences among individuals decrease as the spawning season approaches. Fish with advanced rates exhibit slower development just prior to the spawning season, but development proceeds rapidly in fish with retarded rates.

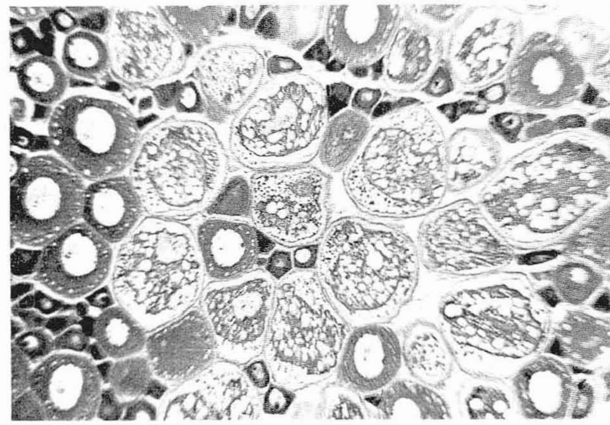

FIGURE 12.—Unspawned eggs being absorbed while new eggs are developing (I-group gizzard shad, December 16, 1953).

Fecundity

The number of eggs per individual varied considerably (table 18). Although the number of counts is meager, the averages for the age groups definitely show low egg production among the precocious I-group shad, a maximum production by the II-group fish, and slowly declining numbers among successively older age groups.

TABLE 18.—*Number of eggs per individual gizzard shad of different sizes and ages*

Age and date of capture	Standard length	Weight	Ovary weight	Estimated eggs per fish	Eggs per gram of fish	Eggs per gram of ovary	Ovary as percentage of fish weight
Age group I:	*Mm.*	*G.*	*G.*	*Number*	*Number*	*Number*	*Percent*
July 6, 1954	225	260	3.9	22,400	86	5,744	1.5
July 8, 1954	236	305	14.8	96,560	317	6,524	4.8
Average	231	283	9.4	59,480	210	6,328	3.3
Age group II:							
May 23, 1955	282	524	78.6	543,910	1,038	6,920	15.0
June 3, 1954	285	529	71.7	524,580	992	7,316	13.6
May 20, 1954	292	593	35.2	211,380	356	6,005	5.9
May 20, 1954	293	578	24.6	258,350	447	10,502	4.3
May 23, 1955	305	526	55.8	356,710	678	6,393	10.6
Average	291	550	53.2	378,990	689	7,124	9.7
Age group III:							
May 23, 1955	322	713	44.5	406,170	570	9,128	6.2
June 18, 1954	328	700	62.6	367,670	525	5,873	8.9
June 24, 1954	343	847	36.2	260,510	308	7,196	4.3
Average	331	753	47.8	344,780	458	7,213	6.4
Age group IV:							
June 18, 1954	348	882	28.8	267,220	303	9,278	3.3
June 23, 1954	363	895	74.2	350,280	391	4,721	8.3
Average	356	889	51.5	308,750	347	5,995	5.7
Age group VI:							
June 23, 1954	355	1,114	29.8	215,330	193	7,226	2.7

As the fish become older, their ovaries acquire increasing amounts of connective tissue; hence, they should produce fewer eggs per gram of ovary with increase in age. This anticipated change is not borne out, however, in table 18. The per-gram-ovary yield of eggs was highly variable, even among the fish of an age group. The situation is not surprising since the problem of finding differences is compounded by the fact that the ovaries were in varying stages of development at the time the fish were captured. An ovary contains a certain number of eggs which would be spawned during the coming spawning season. These eggs, together with immature ones and other components of the ovary, make up the weight of the ovary. The farther along these eggs develop the heavier they become; the weight of the ovary increases and its per-gram yield of eggs decreases.

On the per-gram-of-fish basis the older fish do, indeed, produce fewer eggs than the younger ones (except the precocious I group). The "relative fecundity" tripled from the I group to the II group and then declined to age-group VI which had about the same value as the I group.

On the basis of fish size it would appear that fish weighing 500–600 g. produce more eggs than do those whose weights fall either below or above that range. The productivity of these fish may be the result of age rather than size, however; in the table only the II-group shad occupy this range. Further information on this possibility was gained from 69 II-group female shad, captured in the first two quarters of June 1954; their weights ranged from 339 to 733 g. They were divided by 50-g. groupings (301 to 350, 351 to 400, —), and the ratio of ovary weight to fish weight was calculated for each group. (Egg counts had not been made on these fish.) The ratio was highest for the 500- to 600-g. fish. This finding would suggest, then, that fish in this weight range produce the most eggs.

Spawning

The single spawning site of gizzard shad that I was able to find was a bar some 200 feet long and covered by 2 to 4 feet of water near Put-in-Bay. The bottom is topped with sand, gravel, and boulders. *Cladophora*, *Myriophyllum*, and *Butomus umbellatus* (forma *vallisneriifolius*) are abundant during the spawning season.

No gizzard shad were found on this bar in 1954 prior to, or after, the spawning season. To learn the day-to-day variations of the numbers of shad there during the 1955 spawning season, I set a 100-foot, 4-inch-mesh gill net nightly along the top of the bar from May 9 to June 30. The catches, together with the water temperatures, are recorded in table 19.

It was evident later that the female shad does not spawn her entire egg holdings in one visit to the bar. Consequently, some shad would probably have visited the bar more than once during the season had they not been caught. Furthermore, gizzard shad exhibit greater activity at the height of spawning than just prior to it or afterwards. Hence, greater percentages of those present in a given area are likely to swim afoul of the net at this time than at other periods. The table must be interpreted with these points in mind.

Temperature clearly is important in the onset and progress of spawning. Gizzard shad first appeared in the net on this bar at a temperature of 59° F. and were common at about 67° F. Indeed, when the water temperature dropped slightly (to 65° and 65.5° F. on June 12–15) the numbers of shad also dropped.

To define the spawning site more precisely, I set gill nets transversely across the bar. In every

TABLE 19.—*Water temperatures and daily captures of shad by a 100-foot, 4-inch-mesh gill net set on a spawning site in Fishery Bay in May and June 1955*

[The net was lifted daily at 9 a.m. except on June 2–11 (see text); the water temperature was read at the time of lifting]

Date	Shad caught	Water temperature	Date	Shad caught	Water temperature
	Number	*° F.*		*Number*	*° F.*
May 10	----------	58.0	June 5	12	66.0
11	----------	59.0	6	21	67.5
12	----------	58.5	7	23	66.5
13	----------	60.0	8	24	65.5
14	----------	60.0	9	5	66.5
15	----------	59.0	10	10	66.5
16	----------	61.5	11	16	66.0
17	----------	59.5	12	6	65.5
18	----------	59.0	13	4	65.0
19	1	59.0	14	1	65.5
20	----------	60.0	15	1	65.5
21	----------	61.0	16	14	68.0
22	----------	61.0	17	57	70.0
23	----------	61.0	18	35	71.0
24	----------	61.0	19	38	71.5
25	----------	61.5	20	20	72.0
26	----------	61.0	21	10	71.0
27	----------	62.5	22	10	71.5
28	----------	63.0	23	4	72.0
29	1	63.0	24	33	72.5
30	----------	62.0	25	24	73.0
31	----------	63.0	26	5	73.0
June 1	4	64.0	27	10	74.0
2	6	65.5	28	5	73.5
3	20	67.0	29	18	73.5
4	10	66.0	30	17	73.0

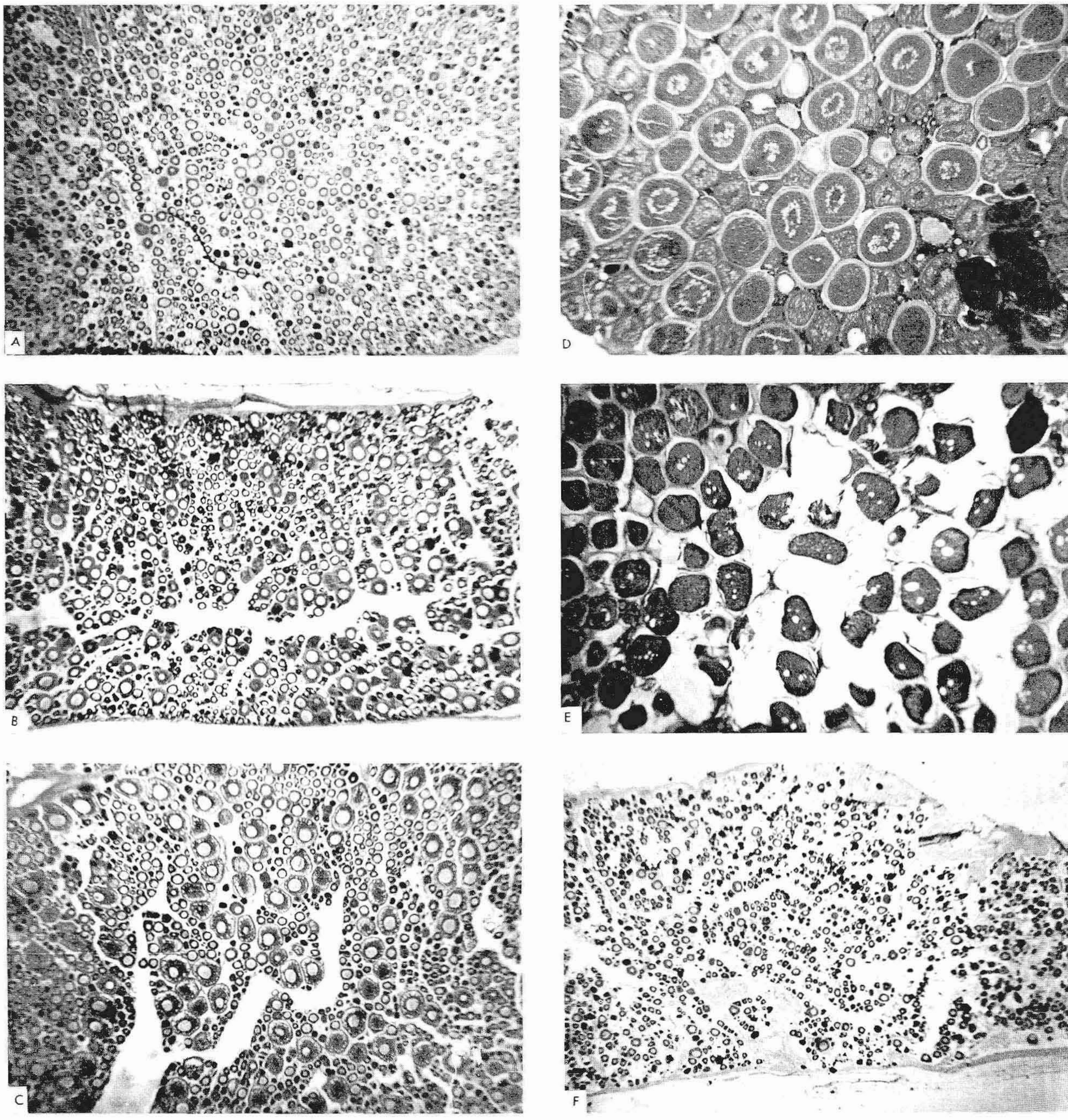

FIGURE 13.—Six stages in the seasonal changes in the ovary of gizzard shad.

lift most of the gizzard shad were caught in that portion of the net that crossed the highest area of the bar, and fewer at the ends of the nets where they sloped gradually into deeper water.

The conditions described here must not be taken as the only ones under which gizzard shad may spawn. Although I have little information on possible shad spawning in the lake, and have never taken shad eggs in plankton nets in the open lake, gill nets and trap nets sometimes have had eggs of gizzard shad and other fish adhering to them during the spawning season. The females may have forced spawn from themselves during their attempts to escape from the gill nets or they may have been held beyond their spawning time in the trap nets, which were lifted only every other day.

It is also probable that some gizzard shad are not able to find a suitable spawning site by the time the eggs are ready to be expelled. This possibility is supported by the observation that some of the female shad caught in the lake by commercial fishermen were releasing eggs. To explore this possibility further, I determined the percentage of spawning fish for the II-group and older female shad caught in Fishery Bay and for those captured in the lake during May, June, and July 1954–55 (table 20). The state of the ovaries was determined by gross examinations. The much smaller percentages of spawning shad captured in the lake than in the bay suggest that most of the ripe females migrated from deeper to shallower water during the spawning season. This finding is not in disagreement with the earlier observation (tables 16 and 17) that the percentage of females in June was less in the shoal water than in the deeper water. The high percentage of males on the spawning reef can be explained on one or more of the logical assumptions that: greater numbers of males than females entered the shoal area from the lake; that activity was greater among the males than among the females in the shoal waters; that males individually stayed longer on the site.

When fish begin to spawn, the rise in the "spawning" category should coincide with the drop in the "nonspawning" category if the fish do not migrate from the area. Lack of this relation in the lake provides further evidence that most of the fish do not remain in the deeper water when they are ready to spawn.

The rapid rise of the "spent" category in the lake from mid-June through July, which is completely out of proportion with the drop in the "spawning" group there, indicates a return of the spent fish from shallow water to the open lake.

The data of table 20 on the percentages of nonspawning, spawning, and spent females captured in Fishery Bay and in the lake during May, June, and July 1954–55 also give a basis for the estimation of the beginning, peak, and end of the spawning season of II-group and older shad.

The earliest samples containing spawning fish were captured in the first quarter of June on the spawning bar in Fishery Bay. The percentage of spawners caught here rose from 33.3 percent in that quarter to a high of 58.3 percent in the next quarter, then dropped to 45.0 percent in the third quarter and abruptly to 1.2 percent in the last quarter of June. Spawning shad were captured from the first quarter of June to the first quarter of July inclusive.

Although I lacked samples from the lake in the first quarter of June (the commercial fishermen of South Bass Island—the source of the lake-caught gizzard shad—did not fish during the last quarter of May and the first quarter of June) the Fishery Bay sample for that quarter and subsequent samples from the lake lead me to assume that spawning fish, though never numerous, were present here at that time also.

Spent fish were first observed in the first quarter

TABLE 20.—*State of ovaries of mature II-group and older gizzard shad captured in Fishery Bay and in Lake Erie in May, June, and July 1954–55*

[Given as percentages of fish in the categories "not spawning," "spawning," and "spent"]

Time of capture	Bay				Lake			
	Females	Not spawning	Spawning	Spent	Females	Not spawning	Spawning	Spent
	Number	*Percent*	*Percent*	*Percent*	*Number*	*Percent*	*Percent*	*Percent*
May:[1]								
1–8	1	100.0	0.0	0.0	32	100.0	0.0	0.0
9–15	7	100.0	.0	.0	44	100.0	.0	.0
16–23	2	100.0	.0	.0	39	100.0	.0	.0
June:								
1–8	51	64.7	33.3	2.0				
9–15	48	37.5	58.3	4.2	34	85.3	8.8	5.9
16–23	40	30.0	45.0	25.0	208	78.8	2.4	18.8
24–30	82	30.5	1.2	68.3	322	44.4	3.1	52.5
July:								
1–8	95	33.6	7.4	59.0	170	38.8	4.7	56.5
9–15	1	100.0	.0	.0	15	33.3	.0	66.7
16–23	2	100.0	.0	.0	14	.0	.0	100.0
24–31					5	.0	.0	100.0

[1] No females captured May 24–31.

of June in the Fishery Bay samples. Thereafter, all samples from both bay and lake showed increasing percentages of spent shad during June. In July, this trend persisted among the lake samples, but in the bay samples both spawning and spent fish were absent after the first quarter and only three nonspawning ones were captured. The available data indicate that the gizzard shad in western Lake Erie spawn during June and early July; the greatest percentage of them spawn in the second quarter of June.

Records of the average ovary weight as a percentage of the fish weight, for II-group and older female shad in 1954–55 (table 21), indicate that the ovary makes little increase in weight from the time the fish are spent until the following April. During that month, feeding increases (this is the first time in winter or spring during which recognizable food has been found in the shad's gut—table 24), but the fish weight decreases (table 9). Consequently, the combination of a little ovarian growth and loss of fish weight results in a rise in the ovary-weight/fish-weight ratio. This ratio is highest either in the last quarter of May, for which I have no samples, or the first quarter of June. In this period, more fish are just ready to spawn and fewer are spawning or are spent than at any subsequent period. Then, as more fish become partly or completely spent, the average ratio drops lower. The drop in June is steady, and in the last quarter of that month the ovary weight as a percentage of body weight is again at about the April level. I have no ovary weights for July, August, and September. However, since some shad are still spawning in

TABLE 21.—*The percentage of fish in the categories "not spawning", "spawning", and "spent", and the ovary weight as a percentage of the fish weight for II-group and older female gizzard shad, Lake Erie, 1954–55*

Period	Fish	Not spawning	Spawning	Spent	Ovary/fish weight
	Number	*Percent*	*Percent*	*Percent*	*Percent*
Oct	25	100.0	0.0	0.0	1.1
Nov	33	100.0	.0	.0	.9
Dec	20	100.0	.0	.0	1.5
Jan	1	100.0	.0	.0	1.1
Feb	4	100.0	.0	.0	1.8
March	1	100.0	.0	.0	1.5
Apr	102	100.0	.0	.0	2.4
May 1-8	33	100.0	.0	.0	3.8
May 9-15	49	100.0	.0	.0	4.2
May 16-23 [1]	41	100.0	.0	.0	4.3
June 1-8	51	64.7	33.3	2.0	9.9
June 9-15	81	58.0	37.0	5.0	8.5
June 16-23	113	47.8	16.8	35.4	5.3
June 24-30	102	16.7	.9	82.4	2.5

[1] No samples May 24-31.

July and follicular remains were yet to be absorbed, I suspect the low percentage of winter samples is not reached earlier than the last of July.

The mature I-group gizzard shad spawn later than older fish. Ova of three fish captured during the 1954 spawning season (June 28, July 6, and July 8) were nearly ripe (fig. 10). These fish probably would have spawned in late July or early August, or else the ova would have been resorbed.

The eggs of the II-group fish which have been in the making for 1½ to 2 years—much longer than those of older fish—might be expected to be spawned earlier than those of older fish. Information on the older shad is too scanty, however, to permit study of this possibility.

The weight of the fish appeared to have no effect on the time of its spawning.

I tried two methods to determine the time of spawning within a 24-hour period. In one, a gill net was set on the previously mentioned spawning bar in the afternoon, lifted at midnight, reset immediately, lifted in the morning, reset again, and lifted in the afternoon. The numbers of shad of each sex were tabulated for each period. In the other method, concrete slabs with a surface area of 1 square foot were lowered to the bottom at the spawning site and examined for shad eggs three times daily, when the gill net was lifted.

Studies by the two procedures covered only 3 days, June 17–19, 1954; in 1955, the net method alone was employed (June 2–11). The gizzard shad spawned most actively in the evening and early night in 1954 and at night in 1955 (table 22); spawning was least in the daytime in both years. I have not seen shad spawning during the daytime, but have seen them milling actively, frequently breaking surface, when I lifted the net at midnight, especially in moonlight.

The individuals participating in the spawning change continually during the season, but a female does not deposit all her eggs during one nightly visit to the bar. Although the percentage of eggs remaining in the ovaries varies among individual fish throughout most of the spawning season, numerous partially spent fish with a substantial percentage of eggs still in the ovary are taken early in the season. Almost none carry large percentages of their eggs toward the close of the season. The state of development of the "nearly mature" ova and the free ones in the ovaries of

TABLE 22.—*Shad eggs and the spawning condition of gizzard shad collected during various periods of the day on a spawning site near Put-in-Bay, Ohio, in June 1954 and 1955*

Dates and period of day	Fish taken by gill nets			Eggs on concrete slabs [1]
	Males	Females		
		Not yet spawned	Partly spent	
	Number	*Number*	*Number*	*Number*
June 17–19, 1954:				
6:30 a.m.–7:30 p.m.	0	2	1	2
7:30 p.m.–12 p.m.	91	16	19	15
12 p.m.–6:30 a.m.	50	7	14	5
June 2–11, 1955:				
9 a.m.–4 p.m.	3	0	0	
4 p.m.–12 p.m.	48	4	7	
12 p.m.–9 a.m.	70	6	9	

[1] No observations in 1955.

spawning gizzard shad indicates possible periods of rest between spawnings.

The males captured on the spawning site during the period of most active spawning outnumbered the females three to one. This abundance of males may be attributed to one or more of the following: Their actual daily recruitment to the spawning site, their probable greater activity, or their possible longer stay on the site. I was unable to distinguish any degrees of "spentness" in the male.

Not having observed details of behavior of spawning gizzard shad, I can offer only the statements of others on spawning behavior. Langlois (1954) observed gizzard shad spawning on May 29, 1935, in North Reservoir at Akron, Ohio, near shore in 6 to 12 inches of water at a water temperature of 67° F. During oviposition, a female was flanked by a male on each side. No time of day was indicated. M. B. Trautman (personal communication) observed about 20 shad spawning in Buckeye Lake, Ohio, at 73° F. on May 23, 1939. The females, pursued by several males, swam rapidly toward a sloping stone wall, turned abruptly, and deposited their eggs. A. G. McQuate (personal communication) observed shad spawning in Sandusky Bay, Ohio, on May 24, 1954 (temperature 62.5° F.), along a stony shore near 12 m. (noon) in the shade of an overhanging tree. Female shad were pursued by several males. The fish frequently broke water.

My own failure to see gizzard shad spawning during the daytime at the spawning site in Fishery Bay can be attributed to their failure to spawn at that time. The small daytime catches in gill nets suggest that shad were extremely scarce at the site. I do not believe they avoided the gear, because the nets were treated with a copper preservative that rendered them greenish and, hence, less visible than untreated nets, and were set in aquatic vegetation which almost wholly obscured them. White bass, smallmouth bass, and rock bass, but very few gizzard shad, were caught in the day.

During the midnight lifts, however, when the moon shone brightly, I saw many fish swirling and breaking water. The moonlight was not bright enough for me to judge accurately the species or size. The gill nets caught many gizzard shad, however, during those nights and had many shad eggs adhering to the webbing. The only other fish caught at those times were a few carp.

Hatching and Early Development

The eggs of the gizzard shad are heavier than water and slowly sink after they are spawned. The egg capsules adhere to surfaces that they contact, such as submerged aquatic plants and stones. Experiments in the Ohio State Hatchery at Put-in-Bay indicated that the hatching time varies from about 36 hours to about a week, depending on the temperature. This finding agrees with Warner's [2] observations at Buckeye Lake, Ohio.

In a series of experimental hatchings over 2 seasons, I failed to keep the young alive beyond the 10th day after hatching. Mortality was low up to the 9th day and the fish appeared to be doing well; then suddenly on the 10th day only a few remained alive out of thousands. The remainder died before the day ended. Results were the same in running and aerated water and with various kinds of food, such as natural food from the lake and cultured protozoans.

The movements of the newly hatched gizzard shad were an upward swimming and a downward settling—in each direction the head was foremost. This behavior continued 3–4 days. The whole body moved sinuously with such rapidity that the individual movements could not be followed. At this time the pectoral fins were not yet used to any extent. On the fourth day the fry began to swim horizontally as well as upward and downward. Their mode of swimming at this age,

[2] Warner, E. N. 1940. Studies on the embryology and early life history of the gizzard shad, *Dorosoma cepedianum* LeSueur. Doctoral thesis, Ohio State University. (Unpublished.)

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observed (in a petri dish) under a dissecting microscope, was largely by the pectoral fins which "vibrated" seemingly with the rapidity of the wings of a bee in flight. The sinuous body movement was not abandoned, but the frequency had slowed enough that it could be followed easily.

When food was added to the aquarium, the young shad darted to and fro as though pursuing some of the small particles. Although the digestive tract contained food during the fifth or sixth day, only green algae were recognized through the thin gut wall.

The young shad congregated on the lighted side of the aquarium. If all sides were lighted, they remained mostly near the source of the running water, facing into the current.

The first few days after hatching, the young gizzard shad subsists on its yolk. Increase in length of the 3.5 mm. newly hatched larva at this time results largely from the straightening of the cephalic flexures, after which the larva attains a length slightly greater than 5 mm. About the 5th day it begins to feed and by the 10th day has attained a length of slightly more than 6 mm. (in the laboratory). At this time it has a filiform shape, which it retains until it has reached a length of 20–30 mm. (fish from the lake—age unknown). Upon reaching this length, the shad begins to increase in depth. The filiform shape gives way to the slab-sided, deep-bodied adult form. Once this shape is acquired the form changes little and the shad begins to grow rapidly.

DIGESTIVE TRACT

Development of the Digestive Tract

The gut of a newly hatched gizzard shad is a tube which conforms to the body curvature. In the 10-day-old larva the gut is a simple, nearly straight tube. Among the older shad the gut of an 18-mm. fish (age unknown) had already developed two flexures (fig. 14). The 19-mm. shad had begun the third and fourth flexures, and the 22.5-mm. fry had already completed them. The portion

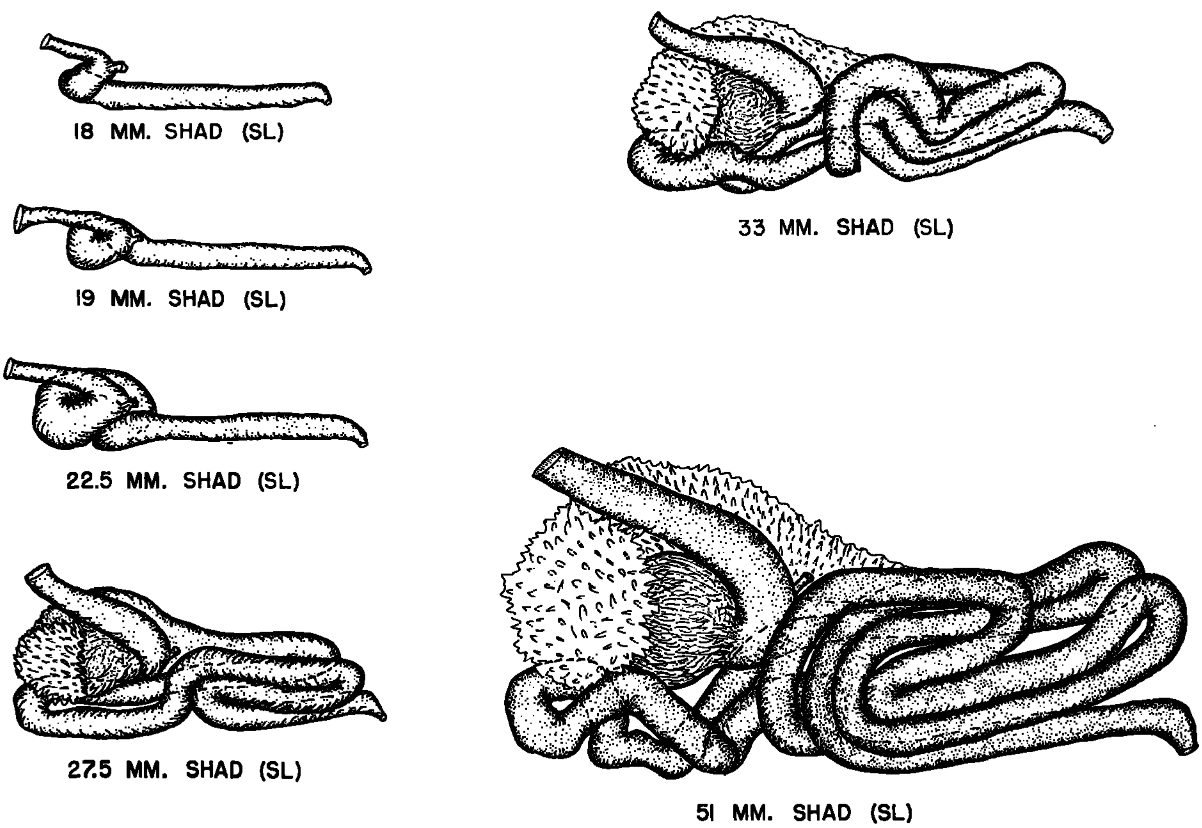

FIGURE 14.—Development of the shad gut (camera lucida drawings).

between the first and second flexures (later to become the gizzard) had enlarged. By the 27.5-mm. stage, the caeca had begun to develop from the duodenum (between the second and third flexures). As the gut continues to grow, the flexures move until they reach the limit of the abdominal cavity. Since the gut grows much faster in length than the abdominal cavity, secondary flexures are produced between the primary ones. Flexures provide landmarks by means of which one can determine relative rates of growth of the different portions of the gut. The caudal portion grows more rapidly and continues to grow over a longer period than any other section. No secondary flexures develop anterior to the third primary one.

Although the course of the gut of a young gizzard shad is complicated, it is relatively simple in comparison with that of the adult of, say, 250 mm., in which the convolutions are so numerous and complex that they defy tracing on a two-dimensional illustration. Indeed, the gut which amounted to one-half of the total length of the day-old fish becomes, in the adult, three times the length of the fish and is packed in an abdominal cavity, one-third of the fish's length.

Forbes (1914) stated that the larva of the gizzard shad has teeth. Although I have examined many young, from newly hatched to longer than 20 mm. (when the adult shape begins to take form), I have not observed teeth.

Digestive Tract in the Adult

The hundreds of long, thin gill rakers of the gizzard shad are admirably adapted for removing particulate matter from the water. This material, especially the filamentous algae and the small crustaceans, apparently is accumulated in the pharyngeal pockets, a paired muscular organ mentioned by Forbes (1888) and described by Lagler and Kraatz (1944). The thick muscular wall and the direct connection with the esophagus suggest that these pharyngeal pouches force their contents into the esophagus. The sphincter muscles in the forepart of the pneumatic duct prevent passage of food into the air bladder.

The muscular esophagus and the gizzard have been described by Wier and Churchill (1945). I can add only that the esophagus possesses longitudinal folds.

Numerous caeca arise in groups on the lateral surface of the duodenum. Each group has a common orifice through which the lumina of its caeca communicate with the lumen of the duodenum. These orifices are arranged in two parallel longitudinal rows. In a 200-mm. shad the lengths of the caeca range from about 5 mm. for those at the anterior end of the row to about 2 mm. at the posterior end. Counts were not made, but an individual appears to possess several hundred caeca. The caeca have internal longitudinal folds. Their lumina are so small that only the smaller unicellular organisms can enter. Although the caeca have the histological appearance of absorptive devices rather than secretory organs, it is only when the duodenum is turgid with food that any material is to be found here.

Wier and Churchill (1945) described a pancreas separate from the liver for the gizzard shad. I have been unable to identify one although I have searched for it repeatedly in many sizes of fish. These authors described the liver as composed of several lobes. I find that it has no definite form in the adult fish but rather seems to spread in close proximity to the gut. The liver invades intercaecal spaces as well as those between neighboring portions of the gut, and completely covers the anterior, dorsal, ventral, and left-lateral surfaces of the gizzard. It is a diffuse organ and intermixed, I believe, with the pancreas.

The small intestine possesses no villi, contrary to the statement of Forbes and Richardson (1908). It does contain four of the large, conspicuous, longitudinal folds described by Wier and Churchill (1945). Attached transversely between the folds and along the inner circumference of the gut are smaller folds or lamellae which have the free edge directed toward the center of the gut lumen (fig. 15). The free edge of each lamella is directed posteriorly at a slight angle. Although the columnar cell covering of these transverse lamellae is unquestionably absorptive and these structures greatly increase the absorptive surface of the gut, they may also function in the manner suggested to me by Milton B. Trautman. He suggested that during peristalsis the longitudinal ridges may lengthen and shorten, thereby causing the lamellae to move back and forth in venetian-blind fashion and, hence, to aid in forcing food along the tract.

This lamellar arrangement within the gut bears some resemblance to the situation described by

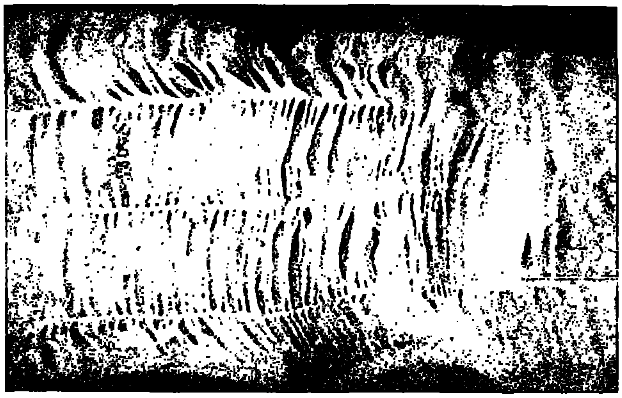

FIGURE 15.—Enlarged view of the small intestine of the gizzard shad showing three of the longitudinal folds with their transverse lamellae.

Kraatz (1924) for the gut of *Campostoma anomalum* in which somewhat similar folds assume a zigzag arrangement.

Transverse lamellae were present in a 22.5-mm. shad. Here they were attached circumferentially to the gut only—the longitudinal folds had not yet formed.

Longitudinal sections of the gut, because they cut across the lamellae, appear to be villous. This fact may account for the statement of Forbes and Richardson that the gut possesses villi.

Digestive Enzymes

Only a qualitative study was made of the digestive enzymes. Attempts to determine their quantity or potency did not yield dependably accurate results. The areas tested were: Pharyngeal pockets, esophagus, gizzard, duodenum (that forepart of the gut bearing the caeca), hepatopancreas, gall bladder, and the first, second, and third portions of the intestine. The materials were prepared in the usual manner and the extraction made with 50 percent glycerol.

Tests were made for the following enzymes: Pepsin, trypsin, amylase, lipase, maltase, sucrase, and rennin. In addition, I sought enzymes that would act on chitin and cellulose.

The enzyme giving the strongest reaction was amylase (table 23). It was present in all areas tested. The reactions for pepsin and trypsin were moderate, whereas the reaction for lipase was weak. I am at a loss to explain the significance of the positive test for rennin.

The presence of enzymes in the esophagus is not restricted to the gizzard shad. Sarbahi (1951) found amylase, maltase, and invertase in the esophagus of the goldfish, and Kenyon (1925) cited Kingsley as reporting gastric glands in the esophagus of the sturgeon.

FOOD AND FEEDING HABITS

The young gizzard shad begins to feed about 4 or 5 days after hatching. The earliest food is probably Protozoa and unicellular algae. When the shad has attained a length of about 20 mm., it feeds on the smaller of the zooplankters and takes practically no phytoplankton. By the time it is 30 mm. long it has assumed the adult shape, and its gizzard is fairly well developed. The fish now begins to feed more and more on phytoplankton.

Three opinions have been offered in the literature regarding the nature of the food of adult gizzard shad. Some believe they eat predominately mud; others insist that they feed almost wholly on

TABLE 23.—*Digestive enzymes found in the gizzard shad*

[If no value is given, a test was not made. The numerical ratings are: 0, negative; 1, not definite; 2, perceptible; 3, small; 4, considerable; 5, strong]

Enzyme	Area tested								
	Pharyngeal pockets	Esophagus	Gizzard	Duodenum	Intestine			Hepato-pancreas	Gall bladder
					1st part	2d part	3d part		
Pepsin	0	3	4	3	0	0	0	2	0
Trypsin	0		0	4				3	2
Amylase	3	3	3	4	4	4	3	5	4
Lipase	0	0	1	2	0	0	0	3	2
Maltase	0	0	0	1	0	0	0	1	1
Sucrase	0	0	0	2	0	0	0	0	0
Rennin	0	0	1	3				3	0
"Chitinase"	0	0	0	0	0	0	0	0	0
"Cellulase"	0	0	0	0	0	0	0	0	0

TABLE 24.—*Monthly record of occurrence of various items in stomach contents of gizzard shad in 1952–55*

Month	Material in digestive tract											
	Debris	Sand	Diatoms	Dinoflagellates	Blue-green algae	Green algae	Protozoans	Rotifers	Ostracods	Copepods	Cladocerans	Insect larvae
Jan	X											
Feb	X											
Mar	X											
Apr	*X	X	X			X		X				
May	*X	X	X			X				X		
June	*X	*X	*X			*X	X	*X		*X	*X	X
July	X	*X	*X	X	*X	*X	X	*X	X	*X	*X	X
Aug	X	*X	*X	X	*X	*X	X	*X	X	*X	*X	X
Sept	X	X	X		X	*X		X		X	X	
Oct	X	X	*X			*X		X			X	X
Nov	X		*X			*X		X		X	X	
Dec	X											

*Indicates the more plentiful items.

phytoplankton; still others maintain that they subsist mostly on zooplankton. All agree, however, that they are "filter-feeders," and this feature alone, I believe, best describes their feeding habits. They filter the water of whatever particulate matter it contains. Shad captured in open waters contained mostly free-floating phytoplankton; those captured among the attached plants, such as *Cladophora*, *Myriophyllum*, and *Ceratophyllum*, ingested Cladocera, Copepoda, Rotifera, and small aquatic insect larvae; those captured in very turbid waters were filled largely with mud. That they do, however, add to their diet from the bottom debris is evidenced by the presence in the gizzard of sand particles of diameters in excess of 0.25 mm. This size of sand is not held in suspension even when the water is highly turbid. Although the bottom is available to the shad at all times, I have not found sand in shad gizzards from December through March. Food particles could not be identified during this period. The taking of sand when food is plentiful suggests its use as an aid in grinding by the gizzard—or it may have been taken accidentally along with food.

The appearance of the food differs in the three distinct regions of the alimentary apparatus—the pharyngeal pockets, the gizzard, and the intestine (especially the forepart which bears caeca and which is often swollen with ingested material). When reference is made to food in the gizzard shad without regard to a definite region of the digestive tract, I use the term "stomach contents."

The pharyngeal pockets, suggested by Lagler and Kraatz (1944) to be accessory to the digestive system, have, to my knowledge, not been thoroughly examined in studies of food of gizzard shad. The pouches frequently are empty, but when food is plentiful and the fish's gut is full of food (especially zooplankton), the pharyngeal pockets contain as much food as the gizzard. The contents of these pockets appear straw-colored and consist mostly of Cladocera and Copepoda along with strands of filamentous algae. Here are found the larger items of the shad's diet, and they are, as yet, not broken apart. The zooplankters still have their full complement of appendages and the filamentous algae are in strands.

The gizzard is frequently empty, and only rarely is it turgid with food. The composition of food in the gizzard is similar to that of the pharyngeal pockets. The zooplankters, however, are more or less dismembered, and the strands of filamentous algae are short. The gizzard contains, in addition, many unicellular algae, rotifers, and some sand along with plant and animal debris.

The intestine usually contains food, although the amount is scanty in winter. Material from the intestine is fragmented and mostly unrecognizable—it has the appearance of bottom debris or mud, especially on gross inspection.

I have found no compact matter exceeding a diameter of 3 mm. in the stomach contents of gizzard shad, except Tendipedidae and small *Leptodora* during certain seasons. Nor have I found in them bits of attached aquatic plants, except after severe storms when small fragments were presumably torn loose and were recovered by the filtering apparatus.

The stomach contents of adult gizzard shad exhibited no appreciable differences among individual shad of a group collected in a locality at the same time. Evidence was lacking for any selection of food within the size range of material they swallow. There were, however, local and seasonal differences related, undoubtedly, to the abundance of the various forms in different places and at different times. As a result of these observations, examination of stomachs of individual fish was soon discontinued and the stomach contents of several fish of a collection were combined.

The feeding habits of gizzard shad were well summarized by Tiffany (1920) who indicated them to be a living tow net. No attempt was made in the present study either to obtain the percentage of each item ingested or to enumerate every organism eaten by the shad at one time or another. In table 24 are listed only major groups of materials found in shad during various months. The table does not identify the months in which the gut contained the most food; in general, the quantity was more plentiful when the diet consisted of a great variety of food in June through November.

Velasquez (1939) cultured algae taken from various parts of the shad gut. As a result either of rapid transit through the gut, or absence of certain enzymes, some algae or certain algae apparently are not utilized as food.

SUMMARY

This study of the life history of the gizzard shad was based on records of the length, weight, and age of almost 24,000 specimens taken in western Lake Erie in 1952–55. Approximate numbers of fish employed in other phases of the study were: calculation of growth from scale measurements, 700; seasonal fluctuations of gonad weight, 700; sex ratio and maturity, almost all fish over 120 mm. long; feeding habits, 200; seasonal development of ovaries, 150; and fecundity, 13.

The fish were captured by means of dip nets, "Common Sense" seines, bag seines, push seine, gill nets of various mesh sizes, regulation commercial trap nets, and by electric shock, dynamite, and rotenone. Fish older than the O-group were captured mostly by the gill nets and trap nets. Most fish were captured within one-half of a mile of the Bass Islands.

The scales of the gizzard shad are described briefly. Two types of annuli are present—a narrow clear-cut line of demarcation and a wider, more evident one. The first annulus is always of the former variety; the second and succeeding ones (with few exceptions) are of the latter variety. The wider, obvious annulus may be a combination of an annulus and a spawning check, while the narrow variety is strictly an annulus.

The time of annulus formation varied with age and sex. Some of the I-group shad began to form the new annulus in May, and all had it by the end of the first quarter of June. Annulus formation of older shad began in June and was completed by mid-July. Females seem to have formed their new annulus about a week earlier than the males. Spawning of these older females occurred while annulus formation was in progress—some fish spawned before the appearance of the new annulus—some after its appearance. Although prespawning development of the gonads was thought to affect the physical appearance of the annulus, the spawning act appeared to have no effect on the time of its appearance. Evidence was given that the annulus is a true year mark.

The body-scale relation was a straight line with an intercept of 22.1 mm. on the axis of standard length.

Calculated lengths showed good agreement with empirical lengths of shad captured between the first of the year and the time of annulus formation—except for the I group. The greater average length of I-group fish at capture can be attributed to gear selectivity.

Sampling problems made the determination of age composition difficult. The young gizzard shad were found in shallow water, the older in deeper water, and the very oldest were captured only during the spawning season. Shad captured in the open lake during fall probably gave the best available estimate of the relative strength of younger age groups. Those captured during the spawning season were most nearly representative of the age composition among the older shad. On these assumptions the following survival from an original 100,000 I-group fish were computed: II-group, 5,534; III-group, 435; IV-group, 63; V-group, 11; and VI-group, 6.

The 1952 year class was one of more than usual abundance. In 1953, as I-group they constituted

85 percent of the fish caught; in 1954, 71 percent as II-group; and in 1955, 11 percent as III-group.

Males made up 45.6 to 49.7 percent of the fish in the four younger age groups (O–III). They were less abundant (36.6 percent) in the age groups IV–VI combined. During the spawning season the percentage of males on the inshore spawning site was greater than normal but that in the open lake was less.

The length-weight relation of gizzard shad varies from year to year, from season to season within the year, according to sex during the spawning season, and among the females according to the state of the ovaries during the spawning season.

Equations were derived for length-weight data and from them was obtained the general length-weight equation, $\log W = -4.81765 + 3.07053 \log L$, in which W is the weight in grams and L the standard length in mm. Gizzard shad from Lake Erie were heavier than those reported from Illinois and Missouri.

Fish of the same length had the greatest weight in August–October. Males were lightest in June; females in May. The spawning-season female was heavier than the male; this difference in weight was not traceable to the gonadal development in the female, but may result from the greater activity of the male at this period. Among the females in the spawning season, those which would not spawn during the current season were the heaviest, those approaching spawning were next, and spent fish were the lightest. The percentage loss in weight during spawning averaged 10.7.

Annual differences in shad weight from relatively heaviest to lightest ran: 1952, 1954, 1955, 1953.

Most of the growth in length for the O-group (which hatched in June) occurred in July–September; for the I-group during June–August; and for the II-group during July–September. Gizzard shad of the II-group and older commence their rapid growth in length about a month later than the I-group fish. Shad lengths remain practically stationary from November until the time of annulus formation.

Males and females had almost the same length at the end of the first year (140 mm.) but after about June of the second year of life the females were consistently longer than males of corresponding ages. The sizes of males and females at the start of different growing seasons were: third, males, 273 mm. and females, 285 mm.; fourth, males, 313 mm. and females, 335 mm.; fifth, males, 343 mm. and females, 364 mm.; sixth, males, 349 mm. and females, 386 mm.

The seasonal growth in weight resembles that of the growth in length except that weight decreases during winter while length remains nearly constant. This loss of weight begins about the start of the year and continues until about May.

Differences among the lengths of individuals of an age group at the end of a calendar year tend to be reduced by later compensatory growth. At the end of succeeding years those fish that were the longest of their year class maintain a length advantage, but this advantage decreases.

The stage of egg development varied from fish to fish throughout most of the year, but with the approach of the spawning season, the retarded shad increased their pace of development while the advanced ones slowed down so that the condition of the ovaries became much more nearly uniform.

A brief description is given of the testis and of various stages of the ovary. The developing egg and the seasonal changes in the saccular ovary also are described.

Not all mature eggs are expelled at the same time. Eggs which are not mature are held over for next year, and those which develop to the spawning stage too late to be expelled are resorbed.

Only rarely were I-group female shad ripe. Most of them (an estimated 80 percent) spawn for the first time as II-group fish. The age of sexual maturity could not be determined for the male; males examined in January had motile sperm—even the new I group. The number of II-group males on the spawning site suggests that most mature as the II-group—the few I-group individuals present may be termed precocious.

A spawning site in the vicinity of Fishery Bay, South Bass Island, was a sandy, rocky bar covered with 2–4 feet of water. Gizzard shad were captured here only during the spawning season—almost all during the evening and night. Spawning was limited in the open lake. The females that are ready to spawn migrate to inshore spawning sites. After spawning, they return to the deeper water. Males also migrate to the spawning sites where they are two or three times as numerous as the females. The representation of the sexes was nearly equal in the open lake at this time. Spawning was most active in the evening and early night in 1954 and in the night in 1955.

Spawning occurred from the first quarter of June through the first quarter of July; peak spawning was in the second quarter of June. The precociously mature I-group fish spawn in late July or later.

The II-group shad produce the greatest number of eggs—about 379,000. In decreasing order are: III-group, 345,000; IV-group, 309,000; VI-group, 215,000; and the precocious fishes of the I-group, 59,000.

On the basis of eggs per gram of fish, relative fecundity triples from age group I to II and then declines to age group VI, which has about the same value as the I group.

The eggs of the shad hatch in 1½ to 7 days, depending on the temperature. The movements of young fry are described.

The gut of a small larva is a nearly straight tube. Sometime after the 10th day the gut begins to fold. The convolutions become more and more complex with increasing size. The gizzard becomes evident in the 22.5-mm. stage. The liver is a diffuse organ, apparently mixed with the pancreas; no pancreas was found.

The intestine lacks villi but has longitudinal folds and transverse lamellae which increase the absorptive surface and may help move the food along during peristalsis.

The presence of sand in the gut when ingested food is plentiful and its absence in winter, when the gut is empty, suggest that it may be taken as an aid in grinding the food in the gizzard.

Food was frequently present in the pharyngeal pockets of large gizzard shad whose gizzard and intestine were packed with food. The presence here of long strands of filamentous algae, and Cladocera and Copepoda with their full complement of appendages, repudiates statements that they are regurgitated into the pockets. In the gizzard, these items were always in some stage of dismemberment.

Tests were positive for the following digestive enzymes: pepsin, trypsin, amylase, lipase, and rennin. Amylase was found in all areas of the tract.

The earliest food of gizzard shad appears to be Protozoa. At a length of about 20 mm., shad feed almost wholly on the smaller of the zooplankters. After the 30-mm. stage, the digestive tract contains greater and greater percentages of phytoplankters. "Filter feeders" best describes the habits of adults. Zooplankters or phytoplankters may predominate in the gut according to their abundance in the water in which the fish are feeding. By the time the food reaches the intestine it has been macerated and partially digested so that it resembles mud. This fact may explain the frequent statement that shad eat mud.

ACKNOWLEDGMENTS

I have had the assistance of the staff members and the students of the Franz Theodore Stone Institute of Hydrobiology, Ohio State University. Thomas H. Langlois suggested an investigation of the gizzard shad in western Lake Erie, made this investigation possible by arranging an Ohio State University Senior Conservation Fellowship, and gave freely of his time in discussing the numerous problems that arose during the study. N. Wilson Britt, Milton B. Trautman, Edward C. Kinney, David Stansbery, and Paul Webster aided in collecting gizzard shad and made helpful suggestions. Jacob Verduin assisted in graphical representations and mathematical interpretations. Ernest Miller, Superintendent of the Ohio State Fish Hatchery at Put-in-Bay, made facilities available for hatching gizzard shad eggs. James W. Moffett, Director of the Biological Laboratory, Bureau of Commercial Fisheries, Ann Arbor, Mich., obtained financial assistance and offered many helpful suggestions. The commercial fishermen—particularly those island fishermen affiliated with Lay Brothers of Sandusky—brought, in samples of shad from their nets. Staff members of District No. 1, Ohio Natural Resources Department, made equipment available. The Ohio Division of Wildlife, through the Onio State University, gave financial assistance. Ralph Hile, Bureau of Commercial Fisheries, Ann Arbor, Mich., read the original manuscript and offered suggestions for its improvement.

LITERATURE CITED

FORBES, S. A.
1888. Studies of the food of fresh-water fishes. Bulletin Illinois State Laboratory of Natural History, vol. 2, pp. 433–473.

FORBES, S. A.
1914. Fresh-water fishes and their ecology. Bulletin Illinois State Laboratory of Natural History, vol. 10, p. 4.

FORBES, S. A., AND R. E. RICHARDSON.
1908. The fishes of Illinois. Natural History Survey of Illinois, State Laboratory of Natural History, vol. 3 (1908), cxxxi+357 pp.

GERKING, SHELBY D.
1945. The distribution of the fishes of Indiana. Investigations Indiana Lakes and Streams, Indiana Department of Conservation, vol. 3, 137 pp.

HILE, RALPH.
1948. Standardization of methods of expressing lengths and weights of fish. Transactions of the American Fisheries Society, vol. 75 (1945), pp. 157–164.

KENYON, WALTER A.
1925. Digestive enzymes in poikilothermal vertebrates. An investigation of enzymes in fishes, with comparative studies on those of amphibians, reptiles, and mammals. Bulletin of the U.S. Bureau of Fisheries, vol. 41, for 1925, pp. 181–200. (Document 977.)

KIRTLAND, JARED P.
1850. Fishes of Ohio. Fragments of natural history. Family Visitor, Cleveland [and Hudson], vol. 1, No. 1, pp. 1–2 (Jan. 3, 1850).

KRAATZ, WALTER C.
1924. The intestine of the minnow, *Campostoma anomalum* (Rafinesque), with special reference to the development of its circling. Ohio Journal of Science, vol. 24, pp. 265–298.

LAGLER, KARL F., AND VERNON C. APPLEGATE.
1943. Age and growth of the gizzard shad, *Dorosoma cepedianum* (Le Sueur), with a discussion of its value as a buffer and as forage of game fishes. Investigations Indiana Lakes and Streams, Indiana Department of Conservation, vol. 2, pp. 99–110, 1942.

LAGLER, KARL F., AND WALTER C. KRAATZ.
1944. Pharyngeal pockets in the gizzard shad, *Dorosoma cepedianum* (Le Sueur). Papers Michigan Academy of Science, Arts, and Letters, vol. 30, pp. 311–320.

LAGLER, KARL F., AND H. VAN METER.
1950. Abundance and growth of gizzard shad, *Dorosoma cepedianum* (Le Sueur), in a small Illinois lake. Journal of Wildlife Management, vol. 15, pp. 357–360.

LANGLOIS, THOMAS HUXLEY.
1954. The western end of Lake Erie and its ecology. J. W. Edwards, Ann Arbor, Mich., 479 pp.

MILLER, ROBERT RUSH.
1957. Origin and dispersal of the alewife, *Alosa pseudoharengus*, and the gizzard shad, *Dorosoma cepedianum*, in the Great Lakes. Transactions of the American Fisheries Society, vol. 86 (1956), pp. 97–111.

MOEN, TOM.
1959. Sexing channel catfish. Transactions of the American Fisheries Society, vol. 88, No. 2, p. 149.

PATRIARCHE, MERCER H.
1953. The fishery in Lake Wappapello, a flood-control reservoir on the St. Francis River, Missouri. Transactions of the American Fisheries Society, vol. 82 (1952), pp. 242–254.

PATRIARCHE, MERCER H., AND EDWARD M. LOWRY.
1953. Age and rate of growth of five species of fish in Black River, Missouri. University of Missouri Studies, vol. 26, pp. 99–105.

SARBAHI, DAYA SHANKAR.
1951. Studies of the digestive tracts and the digestive enzymes of the goldfish, *Carassius auratus* (Linnaeus), and the largemouth black bass, *Micropterus salmoides* (Lacépède). Some anatomical work on digestive tract. Biological Bulletin, vol. 100, pp. 244–257.

SMITH, STANFORD H.
1954. Method of producing plastic impressions of fish scales without using heat. U.S. Fish and Wildlife Service, Progressive Fish-Culturist, vol. 16, No. 2, pp. 75–78.

TIFFANY. L. H.
1920. Algal food of the young gizzard shad. Ohio Journal of Science, vol. 21, pp. 113–122.

TRAUTMAN, MILTON B.
1957. The fishes of Ohio. Ohio State University Press, Columbus, xvii+683 pp.

VAN OOSTEN, JOHN, H. J. DEASON, AND FRANK W. JOBES.
1934. A microprojection machine designed for the study of fish scales. Conseil Permanent International por l'Exploration de la Mer, Journal du Conseil, vol. 9, No. 2, pp. 241–248.

VELASQUEZ, GREGORIO T.
1939. On the viability of algae obtained from the digestive tract of the gizzard shad, *Dorosoma cepedianum* (Le Sueur). American Midland Naturalist, vol. 22, pp. 376–405.

VLADYKOV, VADIN D.
1945. Trois poissons nouveaux pour la province de Quebec. Naturaliste Canadien, vol. 72, pp. 27–39.

WIER, H. C., AND E. P. CHURCHILL.
1945. The anatomy and histology of the digestive system of the gizzard shad (*Dorosoma cepedianum* Le Sueur). Proceedings South Dakota Academy of Science, vol. 25, pp. 34–43.